

S-NA-L [Lawrence]

OCCASIONAL PAPERS

MUS. COMP. ZOOL.
LIBRARY

of the

MUSEUM OF NATURAL HISTORY

The University of Kansas

Lawrence, Kansas

OCT 6 1975

HARVARD
UNIVERSITY

NUMBER 38, PAGES 1-46

SEPTEMBER 10, 1975

A REVIEW OF THE
BROAD-HEADED ELEUTHERODACTYLINE FROGS
OF SOUTH AMERICA (LEPTODACTYLIDAE)

By

JOHN D. LYNCH¹

INTRODUCTION

Most eleutherodactyline frogs are relatively small and nondescript (at least in preservative). However, several species found in forested habitats in northwestern South America and Central America are distinctive in having large, broad heads (head width 45-63 percent of snout-vent length), prominent cranial crests, and in being comparatively large frogs (adult females 30-100 mm SVL). The superficial resemblance of these frogs to *Ceratophrys* has been cited (Dunn, 1944; Rivero, 1961). Most other eleutherodactyline frogs have "narrow" heads (HW/SVL = 30-43%), lack cranial crests, and do not exceed snout-vent lengths of 50 mm. Certain species match the character states of the broad-headed eleutherodactylines for one characteristic but not for all. For example, *Eleutherodactylus anomalus* is more broad-headed than most species (HW/SVL = 41.8-48.3), large (adult females are larger than 50 mm SVL), but lacks cranial crests; *E. curtipes* and *E. galldii* have prominent cranial crests but are smaller frogs (adult females less than 40 mm SVL) with "narrow" heads; in some populations, *E. fitzingeri* is a large frog (adult females 60-75 mm SVL), but all populations have narrow heads and lack cranial crests.

The broad-headed eleutherodactylines include the type species of the genera *Amblyphryne* Cochran and Goin, *Ctenocranius* Melin,

¹ Associate Professor of Zoology, School of Life Sciences, University of Nebraska, Lincoln, Nebraska 68508; Research Associate in Herpetology, Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045.

Limnophys Jiménez de la Espada, and *Strabomantis* Peters. No author has united all the species into a single genus although the idea seems to have been considered at various times (see Rivero, 1961). Fourteen trivial names are available for broad-headed eleutherodactylines. These are disposed in two genera: *Amblyphrynu*s (*ingeri* Cochran and Goin) and *Eleutherodactylus* (*biporcatus* Peters, *bufoniformis* Boulenger, *cornutus* Jiménez de la Espada, *florulentus* Cope, *gulosus* Cope, *koki* Melin, *macrocephalus* Peracca, *maussi* Boettger, *megacephalus* Cope, *napaeus* Jiménez de la Espada, *pelviculus* Cope, *rugosus* Peters, and *sulcatus* Cope).

In Central America, the broad-headed frogs occur from Honduras to Panama. Either two species (*biporcatus* and *bufoniformis*) are recognized or *biporcatus* is fragmented into three species—*biporcatus* (with a single putative synonym, *napaeus*), *florulentus*, and *rugosus* (with three putative synonyms, *gulosus*, *megacephalus*, and *pelviculus*). The Central American frogs are under study by J. M. Savage and further comment on them is restricted to South American populations. I consider the Central American broad-headed frogs as constituting two species, *biporcatus* and *bufoniformis*.

All names applied to South American specimens of broad-headed frogs are currently recognized, with the exception of *napaeus*. I do not consider *napaeus* a synonym of *biporcatus*.

HISTORICAL RÉSUMÉ

Peters (1864) named *Strabomantis biporcatus* from Veragua (= western Panama). He noted the relationships of this frog to *Hylodes* (= *Eleutherodactylus*), in that both groups are partially characterized by having "adhesive" discs on the digits, but separated them because *Strabomantis* had a broad head and narrow interorbital region. The subsequent history of the Central American taxa is summarized by Dunn (1931), Noble (1918), and Taylor (1952). I follow Dunn in recognizing two Central American species of "broad-headed" eleutherodactylines; *biporcatus*, *florulentus*, *gulosus*, *megacephalus*, *pelviculus*, and *rugosus* are considered conspecific.

Jiménez de la Espada (1870) named *Limnophys cornutus* and *L. napaeus* from the Río Suno near San José de Motí, Napo Province, Ecuador. He later (1872) considered *Limnophys* a synonym of *Strabomantis*, *L. napaeus* a synonym of *S. biporcatus*, and *cornutus* to be a valid species of *Strabomantis*. Both species described by Jiménez de la Espada had smooth skin on the venter and coarsely tuberculate skin on the dorsum. The holotype of *L. napaeus* was 50 mm SVL; comparable sized *biporcatus* have nearly smooth skin above and I thus reject Jiménez de la Espada's synonymy of *napaeus* with *biporcatus*.

Cope (1874) named *Hylodes sulcatus* from Nauta, Departamento Loreto, Peru, and considered it "evidently allied to *Strabomantis biporcatus* Peters." *H. sulcatus* differs most conspicuously from *biporcatus*, *cornutus*, and *napaeus*, in having coarsely areolate skin on the venter.

Boulenger (1882) recognized three species of broad-headed eleutherodactylines, *biporcatus* (including *napaeus*), *cornutus*, and *sulcatus*, but placed all of them in *Hylodes* (= *Eleutherodactylus*). Boulenger did not have specimens of any of the named species available; he had a single specimen (BMNH 69.7.25.11) from Bogotá, Colombia, which he referred to *cornutus* and which served as partial basis for his description of the species. He presumed his specimen to be a young specimen of *cornutus* and thus recorded a mosaic of character states based on Jiménez de la Espada's account and BMNH 69.7.25.11. While recording Jiménez de la Espada's characteristic of broad, arched prevomerine dentigerous processes behind the choanae (not the character state in BMNH 69.7.25.11), he also recorded the skin of the venter as areolate. Boulenger also recorded the skin of the venter as granular in *biporcatus*, thus separating Cope's *gulosus*, *megacephalus*, and *pelviculus* (all broad-headed taxa from Central America) from *biporcatus*. Peters' original description of *biporcatus* reads, "Eben so zeigt die Bauchseite kleine Warzchen, während die Kehle glatt ist," and suggests a character state unlike that seen in *sulcatus* or in the BMNH specimen Boulenger referred to *cornutus*, both of which have coarsely areolate skin on the venter. However, Boulenger's error was incorporated into the literature; Nieden (1923) recorded the character state of the skin of the venter in *biporcatus*, *cornutus*, and *sulcatus* as "Unterseite gekornelt" or "Bauch gekornelt."

Boettger (1893) named *Hylodes maussi* from Puerto Cabello, Venezuela; the species has coarsely areolate skin on the venter and was considered allied to *cornutus* and *sulcatus*.

Boulenger (1896) named *Hylodes bufoniformis* from Buenaventura, Colombia. He did not compare *bufoniformis* with other broad-headed eleutherodactylines and some authors have not considered the species allied to the broad-headed complex but have suggested a relationship with the frogs of the *fitzingeri-longirostris* complex (group I of Cochran and Goin, 1970; *binotatus* group of Lynch, 1973).

Peracca (1904) named *Hylodes macrocephalus* from Valle Santiago, Ecuador. This species was another of the frogs with coarsely areolate skin on the venter. Peracca considered it allied to *sulcatus* and distinguished the two taxa on the basis of head shape and the degree of cranial crest development.

Peracca (1914) and Dunn (1944) reported additional Colombian specimens of an areolate-bellied frog with elongate superciliary

tubercles as *cornutus*. Dunn's specimen was later made the holotype of *Amblyphrynx ingeri* (Cochran and Goin, 1961).

Melin (1941) named *Ctenocranius koki* from Taracuá, Brasil. He considered *koki* allied to *cornutus* and *maussi*, and included *cornutus*, but not *maussi*, in the genus *Ctenocranius*. *C. koki* has areolate skin on the venter.

Rivero (1961) regarded *cornutus* (*sensu* Boulenger) and *maussi* conspecific. He suggested that *sulcatus* and *koki* might prove to be conspecific with *cornutus* but noted that *sulcatus* was ". . . described as having an areolate belly." It is unclear if Rivero thought any of the others had smooth bellies; he recorded a granular venter in *maussi*.

My interest in these frogs began with the discovery that *E. cornutus cornutus* of Rivero was very much unlike the illustrations and descriptions given by Jiménez de la Espada (1870, 1875) but in agreement with the descriptions of Cope (1874), Melin (1941), and Peracca (1904). My interest was increased in 1968 when W. E. Duellman secured living specimens matching Jiménez de la Espada's description and figures of *Limnophys cornutus*. Additional specimens of this smooth-bellied frog with a elongate eyelid tubercle were found in the GOV and JAP collections at the National Museum of Natural History and in the collections at the American Museum of Natural History. The areolate-bellied frogs from Andean Colombia are juveniles with well-developed cranial crests and lacking digital pads. In most features they are identical to *Amblyphrynx ingeri*; the differences are assumed to be due to immaturity. The specimen reported by Cochran and Goin (1970) as the second specimen of *Amblyphrynx ingeri* has digital pads, a smooth venter, and numerous other differences from the description of *Amblyphrynx ingeri*; it is an adult female *Eleutherodactylus biporcatus*.

No species of broad-headed eleutherodactylines, other than this latter specimen of *E. biporcatus* were previously known from the Pacific versant and lowlands of South America. Specimens of three species now have been found in the material at the American Museum of Natural History, British Museum (Natural History), National Museum of Natural History, and the University of Kansas Museum of Natural History. Two of these species are smooth-bellied forms (*E. cerastes* new species and *E. necerus* new species) whereas the third is an areolate-bellied frog lacking digital pads (*Amblyphrynx helonotus* new species).

ACKNOWLEDGMENTS

Specimens were loaned by the following curators and their respective institutions. The abbreviations following the name of the institutions are used throughout the text to identify particular specimens. James Bölkhe, Academy of Natural Sciences, Philadelphia

(ANSP); James R. Dixon, Texas Cooperative Wildlife Collection, Texas A and M University (TCWC); William E. Duellman, University of Kansas Museum of Natural History (KU); Alice G. C. Grandison, British Museum (BMNH); Birgitta Hansson, Göteborgs Naturhistoriska Museum (GNM); Rogert F. Inger and H. Marx, Field Museum of Natural History (FMNH); Richard Mount and Terry Schwaner, Auburn University Museum (AUM); Umberto Parenti, Museo de Istituto di Zoologia Sistematica della Università di Torino (MZS); the late James A. Peters and George Zug, United States National Museum (USNM); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Ernest E. Williams, Museum of Comparative Zoology (MCZ); John Wright, Los Angeles County Museum (LACM); and Richard G. Zweifel and Charles W. Myers, American Museum of Natural History (AMNH). William E. Duellman took photographs of living frogs, checked the Madrid collection for Jiménez de la Espada's types, and has generously undertaken field work in my behalf in quest of these frogs. Charles W. Myers loaned a photograph of a rare species. The University of Nebraska Research Council provided funds enabling me to study at the United States Museum and the British Museum (Natural History). James A. Peters and Alice Grandison provided working space at their respective institutions. Juan León provided a Spanish summary for the paper. My thanks go to all.

TAXONOMIC CHARACTERISTICS

The primary characteristics of the broad-headed eleutherodactylines are head width and the presence of cranial crests. This combination of characteristics occurs in the nine species here termed "broad-headed eleutherodactylines" as well as in another telmatobiine genus, *Proceratophrys* (Odontophrynnini). The leptodactylids of the subfamily Ceratophryinae (Lynch, 1971) have broad heads (HW/SVL = 45-65%) but lack cranial crests.

Head width/snout vent length (HW/SVL).—The range of this feature among eleutherodactyline frogs is 29.9-62.8%. The distribution of HW/SVL values for eleutherodactyline frogs is bimodal; a pronounced mode is centered at about 36-38%, a smaller one at about 49-50%. Percentages at around 50% apply to the frogs here termed "broad-headed"; the species and the ranges of HW/SVL for each are (N for each sample is given parenthetically following the range):

<i>A. helonotus</i> new species	49.5-51.0(2)
<i>A. ingeri</i>	55.1-62.8(3)
<i>E. biporcatus</i>	47.9-54.3(27)
<i>E. bufoniformis</i>	44.4-58.2(22)
<i>E. cornutus</i>	48.8-56.4(7)

<i>E. cerastes</i> new species	45.8-52.8(15)
<i>E. maussi</i>	44.3-54.9(10)
<i>E. necerus</i> new species	46.2-49.7(3)
<i>E. sulcatus</i>	45.6-53.3(15)

The following three species of *Eleutherodactylus* are annectant between "broad-headed" and "narrow."

<i>E. anomalus</i>	41.8-48.3(21)
<i>E. lymani</i>	35.7-44.5(16)
<i>E. taurus</i>	40.8-45.3(8)

The category of "narrow" head widths includes the following examples.

<i>E. achatinus</i>	33.5-43.2(156)
<i>E. chloronotus</i>	33.9-42.2(28)
<i>E. conspicillatus</i>	36.2-42.0(36)
<i>E. curtipes</i>	29.9-40.6(461)
<i>E. surdus</i>	33.6-40.8(28)
<i>E. unistriatus</i>	34.8-39.4(40)
<i>E. variabilis</i>	30.7-37.2(20)
<i>E. w-nigrum</i>	33.7-40.2(77)
<i>Phrynoporus</i> (13 spp)	31.1-40.8(282)
<i>Syrrhophus</i> (14 sp)	30.8-42.4(338)

All of the "broad-headed" taxa have cranial crests, although those of *E. bufoniformis* are not as well-developed as those of some broad-heads, e.g., *E. biporcatus* or *E. sulcatus*. None of the annectant taxa have cranial crests whereas the occurrence of cranial crests among the frogs with "narrow" heads is sporadic—the presence of crests is interspecifically variable (e.g., in *Phrynoporus flavomaculatus*, *P. parkeri*, and *P. pereger*).

The South American specimens of broad-headed eleutherodactylines appear to represent nine species. Each can be diagnosed on the basis of color patterns, proportions, and a suite of other characteristics. The color patterns are distinctive but difficult to use for grouping taxa. Most of the other characteristics can be used to group species and thus provide data for an analysis of intragroup relationships among broad-headed eleutherodactylines.

In addition to coloration, the characteristics useful in species discrimination are as follows:

- 1.—Texture of skin of dorsum. The arrangement of tubercles and folds, while difficult to describe, can be used in species recognition; the degree of tubercularity is ontogenetically variable within *E. biporcatus*.
- 2.—Texture of skin of venter. The venter is either coarsely areolate (granular) or smooth. The character shows no intraspecific variation.

- 3.—Eyelid tuberculation. The eyelid is tubercular in all species but some forms have one or two elongate posterolateral eyelid tubercles.
- 4.—Tarsal fold. An inner tarsal fold is consistently present in some species.
- 5.—Digital discs. Three character states are consistent. No digit bears discs; discs (on the ventral surface of the digit, bounded by a circumferential groove) are present on the toes but not the fingers; or, discs are present on the fingers and toes.
- 6.—Ulnar tubercles. The posterolateral edge of the forearm may bear a series of large, crest-like warts or a series of smaller, less prominent tubercles. This feature varies with the size of the animal and is thus of limited value.
- 7.—Supernumerary plantar tubercles. Prominent supernumerary plantar tubercles occur in the adults of only two species. Juveniles of at least one another species are known to have these tubercles but they are absent in adults. The feature is thus of limited value.
- 8.—Lateral fringes on digits. If present, lateral fringes are most prominent on the toes. The lateral fringes are never flap-like, as in *Hylodes* (Elosiinae), but are easily recognized in juveniles and adults.
- 9.—Basal webbing. This trait is recorded as "toes free" if the webbing does not enclose the basal subarticular tubercles of the toes, and "webbed" if the basal subarticular tubercle is enclosed. A single species has basal webbing.
- 10.—Metatarsal tubercles. All specimens have two, and the inner is more prominent than the outer. Some species have an obscure outer tubercle and a prominent, laterally compressed inner tubercle, whereas others have a small, but prominent outer and a larger, non-compressed inner metatarsal tubercle.
- 11.—Flaring of the lips. Only specimens from Venezuela and the Amazon basin have prominently flared lips as juveniles and adults. Adults and juveniles of all other taxa have little or no flaring of the lips.
- 12.—Snout profile. In lateral profile the snout is either strongly sloping, weakly sloping, or truncate. The difference between "weakly sloping" and "truncate" is not consistent within a species.
- 13.—Prevomerine processes. Two character states are evident—triangular in outline or broad and arched (lateral edge reaches to outer edge of choana). Ontogenetic variation seen is in one species: triangular as juveniles, arched as adults. The characteristic is thus of limited value.

- 14.—Vocal slits. The males of most species have vocal slits but in two species males evidently lack vocal slits. In each case, the males are small. Males are not available for all species and the characteristic is thus of limited value.
- 15.—Cranial crests. All species have crests on the frontoparietal bones. In adults, the crests are lateral (and largely parallel) or parasagittal (and converging). In two species, there is some evidence of the crests extending onto the nasals. In most species, the crests are absent or obsolete in juveniles; the characteristic is thus of limited value.
- 16.—Temporal region. The infratemporal fenestrum is occluded by bone (squamoso-maxillary contact) in the holotype of *Amblyphrynx ingeri*. In all other specimens, including juvenile *A. ingeri*, the squamosal is not in contact with the maxillary.
- 17.—Osteoderms. The holotype of *A. ingeri* has osteoderms in the skin of the dorsal surfaces. No other specimen, including juvenile *A. ingeri*, has detectable osteoderms.
- 18.—Tympanum size. No difference in ear size among juveniles and males and females occurs in some species, whereas in other species (e.g., *E. biporcatus*) males have much larger tympana than do females. Because male specimens are lacking for some species and ontogenetic series are not available for all species, the feature is of limited value.
- 19.—Shank length. The variation of shank length within species renders this feature of questionable value. Some species have short legs (*Amblyphrynx*), whereas others are comparatively long-legged (*E. cornutus*); but, the differences are not diagnostic.

Characteristics in which a character state is unique to one species are of limited value in discerning relationships. For a characteristic to be of value, each character-state must be represented in two or more taxa. Likewise, characteristics in which the character-states change ontogenetically within a putative species are of little value unless comparisons are made only among individuals of the same sex and age. Therefore, of the above characteristics, only numbers 2, 3, 4, 5, 8, 10, 11, and 12 are available for comparison of taxa.

Texture of venter (2).—Cope (1866) distinguished *Hyloides* and *Lithodytes* on the basis of the texture of the skin of the venter. Under Cope's system, *Hyloides* included the frogs with digital discs having areolate skin on the venter and *Lithodytes* included those with discs and smooth skin on the venter. Jiménez de la Espada (1870) diagnosed *Limnophys*, and later (1872) *Strabomantis*, on the basis of smooth skin on the venter.

The broad-headed taxa with smooth skin on the venter are *biporcatus*, *bufoniformis*, *cornutus*, *florulentus*, *gulosus*, *megacephala*,

lus, *napaeus*, *pelviculus*, and *rugosus*. Those with areolate skin on the venter are *ingeri*, *koki*, *macrocephalus*, *maussi*, and *sulcatus*. One undescribed species (*helonotus*) has areolate skin on the venter and two (*cerastes* and *necerus*) have smooth skin on the venter.

Poorly preserved specimens of areolate-venter taxa sometimes superficially appear to have smooth skin on the venter. Examination under magnification reveals the true character-state. Of greater difficulty is distinguishing a superficial areolation in smooth-venter taxa. In these examples the "warts" appear to be due to an effect of preservatives and are spinule-like rather than the pavement-like texture seen in frogs having areolate skin on the venter. The problem is most severe in small frogs (less than 25 mm SVL).

Eyelid tubercles (3).—All species of broad-headed eleutherodactylines have tubercles on the upper eyelids. The character-states used in distinguishing taxa reflect not the presence of tubercles but the relative lengths of the tubercles. All specimens here assigned to *cerastes*, *cornutus*, and *ingeri* have elongated tubercles (Fig. 1) at

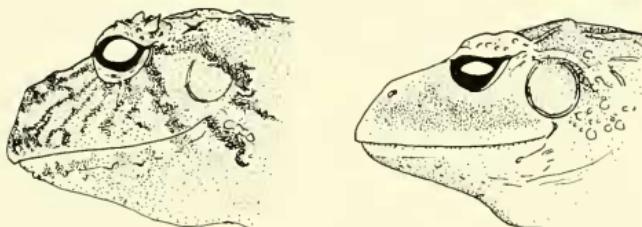


FIG. 1.—Lateral profiles of heads of *Eleutherodactylus cornutus* (left, KU 123448) and *E. maussi* (right, UMMZ 113940, AB 4496).

the posterolateral corner of the upper eyelids. The tubercles are evident in juveniles as well as large adults. Jiménez de la Espada (1870) recorded shorter tubercles in *napaeus* than in *cornutus*; he illustrated (1875) only *cornutus*, so it is not possible to determine if *napaeus* had distinct horn-like eyelid tubercles such as occur in *cerastes*, *cornutus*, and *ingeri* or whether the eyelid tuberculation was wart-like, such as that seen in *biporcatus*, *bufoniformis*, *koki*, *macrocephalus*, *maussi*, or *sulcatus* (Fig. 1).

Tarsal fold (4).—An inner tarsal fold is found in the Amazonian (*cornutus*, *koki*, *macrocephalus*, *sulcatus*) and Andean (*ingeri*, *maussi*) taxa but not in those from the Pacific versant or lowlands or those from Central America.

Digital discs (5).—Two species (*helonotus* and *ingeri*) lack discs on the digits. The disc is the structure on the ventral surface of the digital tip surrounded by a groove; the groove is most distinct at the tip of the digit. I use the term "digital pad" for any apical dilation of the digit. The nominal species *koki*, *macrocephalus*, and *sulcatus* have discs on the toes but none on the fingers although the fingers

may have apical swelling and some dilation (Fig. 2). All other broad-headed taxa have discs on the fingers and toes. In all species the tips of the toes are broader (and pad-like) than those of the fingers.

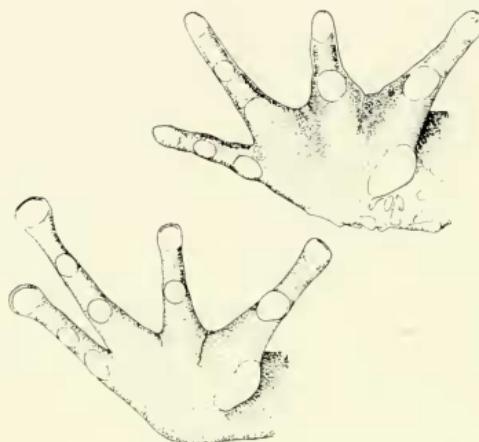


FIG. 2.—Palmar views of hands of *Eleutherodactylus biporcatus* (left, KU 108426) and *E. sulcatus* (right, KU 126171).

Supernumerary plantar tubercles (7).—*koki*, *macrocephalus*, *maussi*, and *sulcatus* have prominent supernumerary plantar tubercles; I also found less prominent tubercles on the plantar surfaces of young *ingeri*. No adult broad-headed eleutherodactyline except *maussi* and *sulcatus* has supernumerary plantar tubercles.

Lateral fringes on digits (8).—The fingers lack basal webbing, and even when present, lateral fringes on the fingers are difficult to detect (Fig. 2). Lateral fringes on the toes are readily detected. Most South American broad-headed taxa have lateral fringes; fringes are absent in *biporcatus* and *cerastes*.

Metatarsal tubercles (10).—All specimens examined have two metatarsal tubercles and the inner is larger than the outer. The inner metatarsal tubercle is strongly compressed laterally and the outer obscure in *biporcatus*, *bufoniformis*, and *necerus*. In the other species the inner tubercle is not compressed, or has only slight lateral compression, and the outer is more prominent (Fig. 3).

Flaring of the lips (11).—The loreal region is more vertical in *biporcatus*, *bufoniformis*, *cerastes*, *cornutus*, *ingeri*, and *necerus*, than in *koki*, *macrocephalus*, *maussi*, and *sulcatus*. In the latter group of taxa, the snout is strongly sloping in lateral profile (Fig. 1), a feature not seen in the other broad-headed taxa. Associated with flaring of the lips is the flaring of the posterior maxillary arch. The frogs with posterior flaring have an obliquely oriented tympanum. The increase in slope of the temporal region increases ontogenetically (Fig. 4) so that young frogs have nearly vertical tympana

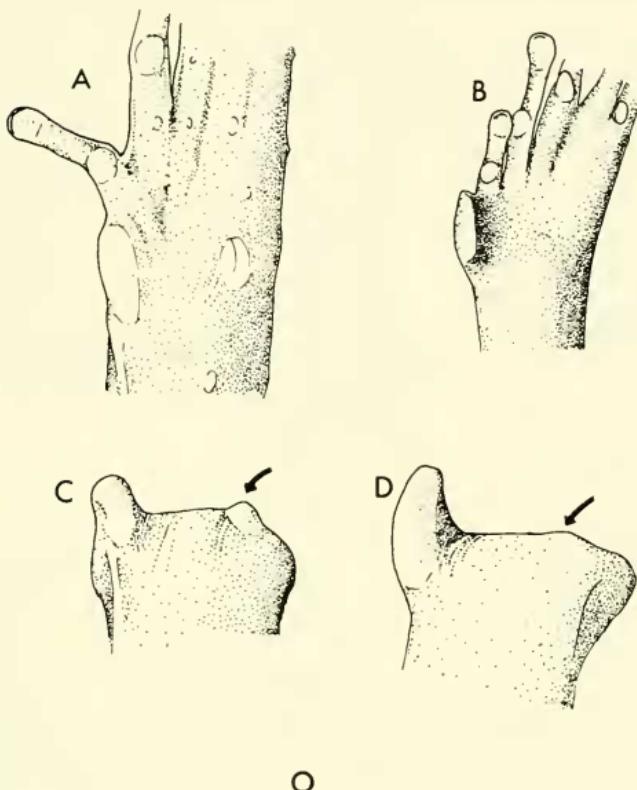


FIG. 3.—Proximal portions of feet of (A) *Eleutherodactylus cornutus*, KU 123448, and (B) *E. biporcatus*, KU 108425, and plantar level views of metatarsal tubercles of (C) *E. cornutus*, KU 123448, and (D) *E. biporcatus*, KU 108425. Arrows point to outer metatarsal tubercles.

whereas large adults (especially females) have markedly oblique tympana. The slope of the tympanum was used by Peracca (1904) to distinguish *macrocephalus* from *sulcatus*; the distinction is size-related—the holotype of *macrocephalus* is 35 mm SVL, that of *sulcatus* 47 mm SVL.

Prevomerine processes (13).—All specimens of broad-headed eleutherodactylines have prevomerine teeth, but the shape of the prevomerine processes varies from triangular to arched (Fig. 5). The processes are triangular in all Central American frogs (nominal species *biporcatus*, *florulentus*, *gulosus*, *megacephalus*, *pelviculus*, and *rugosus*) as well as *bufoniformis*, *ingeri*, and the small specimens of *necerus*. The processes are arch-like (extending laterally to the middle or external edge of the choanae) in adult *necerus*, and all specimens of *cornutus*, *helonotus*, *koki*, *macrocephalus*, *maussi*, *nappaes*, and *sulcatus*. The holotype of *sulcatus* and a second Peruvian specimen (AMNH 43391) are the only exceptions; in both specimens, the lateral extent of the prevomerine processes is the median

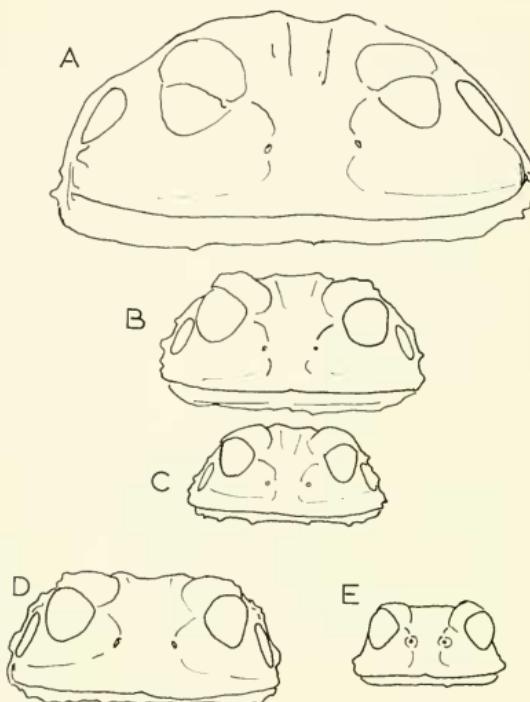


FIG. 4.—Outline drawings of anterior view of heads of *E. maussi*, (A) AMNH 70549, 67.9 mm SVL; (B) AMNH 70546, 36.4 mm SVL; (C) AMNH 70548, 25.0 mm SVL; (D) AMNH 70542, 22.0 mm SVL; and (E) AMNH 70536, 12.7 mm SVL.

border of the choanae. The narrow processes of these two examples are considered abnormal, but the occurrence of such variation mitigates the value of the feature.

Triangular prevomerine processes are found in most frogs of the *binotatus* group. No eleutherodactyline frogs from South America except some broad-headed taxa have arched processes. Arched processes are known among West Indian *Eleutherodactylus* (*inoptatus* and *ricordii* groups) and in most *Leptodactylus*.

Cranial crests (15).—The cranial crests are borne on the fronto-

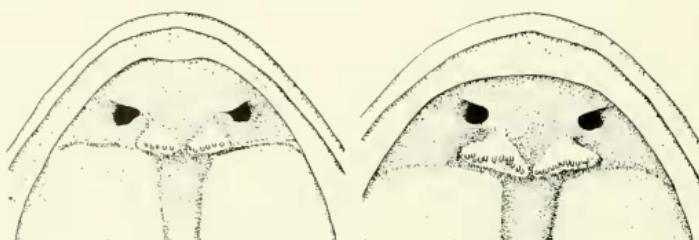


FIG. 5.—Anterior palates of *Eleutherodactylus bufoniformis* (left, KU 113787) and *E. sulcatus* (right, AMNH 43136).

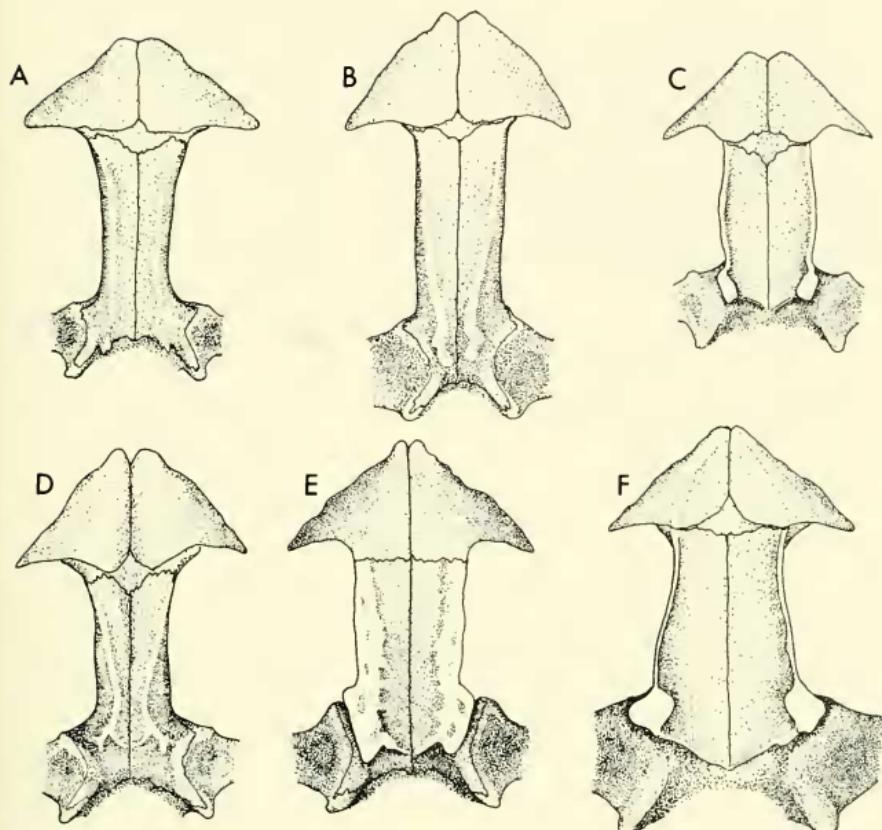


FIG. 6.—Roofing bones (and portions of neurocrania) with cranial crests of (A) *Eleutherodactylus bufoniformis*, KU 80621, (B) *Amblyphryne helonotus*, BM 1970.178, (C) *E. biporcatus*, LACM 73157, (D) *E. cerastes*, KU 144992, (E) *E. sulcatus*, AMNH 52856, and (F) *A. ingeri*, AMNH 39979.

parietals and are either lateral (Figs. 6C, E and F) or parasagittal (Figs. 6A, B, and D). Most species have lateral crests; parasagittal crests occur in *bufoniformis*, *cerastes*, *helonotus*, and *necerus*. In young *biporcatus* and *sulcatus* the crests are somewhat parasagittal; in larger frogs they become lateral. Crests are poorly developed and nearly indistinguishable in juveniles and young males of *maussi*; in general, crests of males are less well-developed than those of females.

In *ingeri* and, to a lesser extent, *sulcatus*, the crests continue onto the nasal bones. I did not find crests on the nasals of any other specimens examined, but Cope (1875) reported the crests extending onto the nasals in the holotype of *Lithodytes gulosus*. Posteriorly, the crests terminate in an enlarged knob or boss in large specimens. The boss is most prominent in large *biporcatus* (Fig. 6C) and in juvenile *ingeri* (Fig. 6F). In all examples with crests, the crests are higher posteriorly and approximate an elevated boss.

The otic ramus of the squamosal forms a crest in some examples.

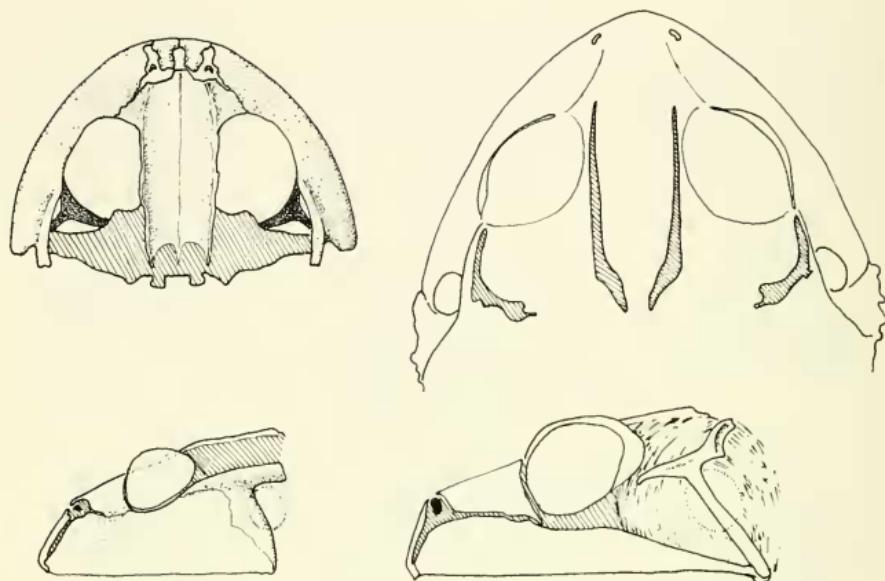


FIG. 7.—Left: reconstruction of skull of *Amblyphrynum ingeri* based on radiographs (FMNH 81915). Top right: outline drawing of head of *Eleutherodactylus biporcatus* (hatching indicates position and shape of cranial crests). Lower right: lateral view of head of *E. biporcatus* (LACM 73157) showing extent of bones and position of tympanum.

The otic crest is most pronounced in *Amblyphrynum ingeri* (Fig. 7) but detectable crests are also found in larger examples of *maussi* and *sulcatus*. A crest-like keel is found on the otic ramus of the squamosal in large adult female *biporcatus*; the keel is not parallel to the cranial crests as in *ingeri* (Figs. 6-7) and *sulcatus*.

KEY TO BROAD-HEADED ELEUTHERODACTYLINES

1. Digits lacking discs 2
At least toes bearing discs (defined by circumferential grooves) 3
2. Tarsus bearing fold along inner edge; cranial crests prominent ending posteriorly in large boss *Amblyphrynum ingeri*
Tarsus lacking folds; cranial crests obscure, no enlarged boss posteromedial to eyes *Amblyphrynum helonotus*
3. Skin of venter coarsely areolate 4
Skin of venter smooth 5
4. Fingers lacking discs; posterior surface of thighs with large pale spots *Eleutherodactylus sulcatus*
Fingers bearing discs; posterior surface of thighs uniform brown *Eleutherodactylus maussi*

5. Upper eyelid bearing elongate tubercle at posterolateral corner	6
Upper eyelid lacking elongate tubercles	7
6. Tarsal fold present; toes bearing lateral fringes	
	<i>Eleutherodactylus cornutus</i>
Tarsus lacking folds; toes lacking lateral fringes	
	<i>Eleutherodactylus cerastes</i>
7. Toes lacking lateral fringes	
	<i>Eleutherodactylus biporcatus</i>
Toes bearing lateral fringes	8
8. Basal subarticular tubercles of toes enclosed by webbing	
	<i>Eleutherodactylus bufoniformis</i>
Basal subarticular tubercles of toes not enclosed in toe webbing	
	<i>Eleutherodactylus nigerus</i>

SYSTEMATIC ACCOUNTS

The published descriptions of *E. biporcatus*, *E. bufoniformis*, *E. maussi*, and *E. sulcatus* are adequate and not duplicated here. For these taxa I have provided an extensive diagnosis and definition as well as references to published descriptions. Because altitudinal data are not available for the majority of specimens, I have used general statements for the elevational distributions, viz., low (0-800 m), moderate (800-1600 m), and intermediate (1600-2500 m).

The fourteen nominate species of broad-headed eleutherodactyline frogs and three undescribed species are placed in two genera—*Amblyphrynyus* and *Eleutherodactylus*.

Amblyphrynyus Cochran and Goin

Diagnosis.—Eleutherodactyline frogs with simple digits (no pads or discs; terminal phalanges knobbed) and broad-heads (HW/SVL:50-63%).

These frogs have areolate skin on the venter, the first finger longer than the second, lateral fringes on the digits, no webbing of the digits, prominent prevomerine dentigerous processes, prominent, externally visible, tympana, cranial crests, and a cartilaginous omosternum. The nasals and frontoparietals are in broad median contact.

Type-species.—*A. ingeri* Cochran and Goin, by original designation.

Content.—Two species found in northwestern South America.

Amblyphrynyus ingeri Cochran and Goin

Fig. 8

Hylobates cornutus (part): Boulenger, 1882:220; Peracca, 1914:107.

Eleutherodactylus cornutus: Dunn, 1944:26; Cochran and Goin, 1970:442.

Amblyphrynyus ingeri Cochran and Goin, 1961:543; 1970:360. [Holotype.—

FMNH 81915, 8 km S Gachalá, San Isidro, Cundinamarca, Colombia, 2350 m].

Diagnosis.—A large eleutherodactyline frog (one adult ♀ 50 mm SVL) with heavy lateral cranial crests on the frontoparietals; skull with extensive exostosis (nasals, frontoparietals, maxillae, squamosals); squamosal broadly contacting maxilla, no opening between squamosal, maxilla, and quadratojugal in adult female; prevomerine dentigerous processes triangular in outline, postero-medial to choanae; skin of dorsum bearing osteoderms; skin of dorsum weakly tuberculate in adult female (no large flat warts), coarsely tuberculate in juveniles; upper eyelid bearing elongated tubercle on posterolateral surface; tarsal fold present; venter uniform brown.

Description.—Cochran and Goin (1961, 1970) have described the holotype (the only known adult). A description of juvenile frogs (20.0-25.0 mm SVL) is provided here.

Head broader than body, wider than long; head width 58.9-62.8% ($\bar{x} = 60.8$) SVL; snout round in dorsal view, short and truncate in lateral profile (Fig. 8); length of eye greater than distance between eye and nostril; canthus rostralis sharp, straight or slightly concave; loreal region somewhat concave, sloping gradually to lips; lips flared; nostrils protuberant, directed laterally; tip of snout not bearing proboscis or ridge, not extending much beyond lower jaw; interorbital region concave, edges of frontoparietals enlarged to form cranial crests; interorbital region broader than width of upper eyelid; upper eyelid 75.0-88.9% ($\bar{x} = 80.3$) interorbital distance; upper



FIG. 8.—Juvenile *Amblyphryne ingeri*, AMNH 39979.

eyelid bearing elongate superciliary tubercles; cranial crests terminate posteriorly in bosses lying posteromedially to eyes; anteriorly they form canthus rostralis; tympanum prominent, exposed, slightly higher than long, its horizontal diameter 56.1-66.7% length of eye in females, 84.3% in one male; supratympanic fold present, bearing tubercles; edges of lower jaw tuberculate; tongue large, fleshy, posterior one-fifth free, not notched posteriorly; choanae relatively small, oval, completely visible when roof of mouth is viewed from directly below; prevomerine dentigerous processes present, round, each

bearing a clump of 4-5 teeth, each process about twice as large as a choana; males lacking vocal sac and vocal slit.

Skin of dorsum pustular and bearing enlarged ridges and tubercles; tubercles prominent on eyelids, on interorbital region, and tending to form ridges on back; limbs tuberculate and ridged; tubercles and ridges less prominent on upper arm and thighs than on forearm, shank and tarsus; skin of venter coarsely areolate; discoidal folds indistinct, terminating posteriorly well anterior of thighs; shank 52.0-54.5% ($\bar{x} = 53.4$) SVL; outer edge of forearm bearing enlarged ulnar tubercles which tend to coalesce to form ulnar ridge; no enlarged tubercle on elbow; two palmar tubercles, outer and median largely fused (Fig. 9); thenar tubercles as large as subarticular

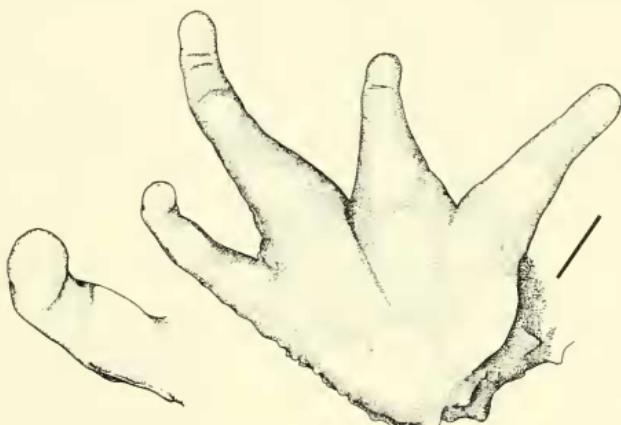


FIG. 9.—Palmar view of hand of *Amblyphryne ingeri* (AMNH 39978). Line equals 1 mm. The fourth finger is enlarged 2 \times at the left.

tubercles, pale in color; subarticular tubercles round, simple, somewhat conical; no supernumerary tubercles on digits; digits bearing slight lateral fringes; tips of digits not enlarged to form distinct pads, lacking circumferential groove at tips (Fig. 9); first finger distinctly longer than second, heel not bearing enlarged tubercles; outer edge of tarsus bearing a row of enlarged tubercles extending from heel to outer metatarsal tubercle; inner surface of tarsus bearing a weak inner tarsal fold extending from inner metatarsal tubercle proximally for about $\frac{1}{2}$ to $\frac{2}{3}$ length of tarsus where it is replaced by a row of enlarged tubercles; inner metatarsal tubercle not compressed, about three times as long as wide and about three times as large as round, non-conical outer metatarsal tubercle; plantar surface bearing numerous supernumerary tubercles arranged in rows approximately corresponding to metatarsal bones; subarticular tubercles of toes smaller than those of fingers, round, flat, simple; tips of toes bearing small pads, about as long as wide; toes bearing ill-defined lateral

fringes but lacking webbing; outer edge of foot and fifth toe bearing a tuberculate ridge.

Coloration in preservative.—Body brown with dark brown to black markings (canthal stripe, supratympanic stripe, labial bars, bars on limbs and edges of scapular ridges); posterior surface of thigh pale brown with numerous small, pigmentless spots; anterior face of thigh and lower flanks bear small pigmentless spots.

Distribution.—Andes of Colombia at intermediate elevations (Fig. 10). Two literature records of *Eleutherodactylus cornutus* based on specimens not seen by me are believed to apply to *A. ingeri*. These are Peracca's (1914) frog from Camelia, Depto. Antioquia Colombia, 1720 m, and Cochran and Goin's (1970) frog

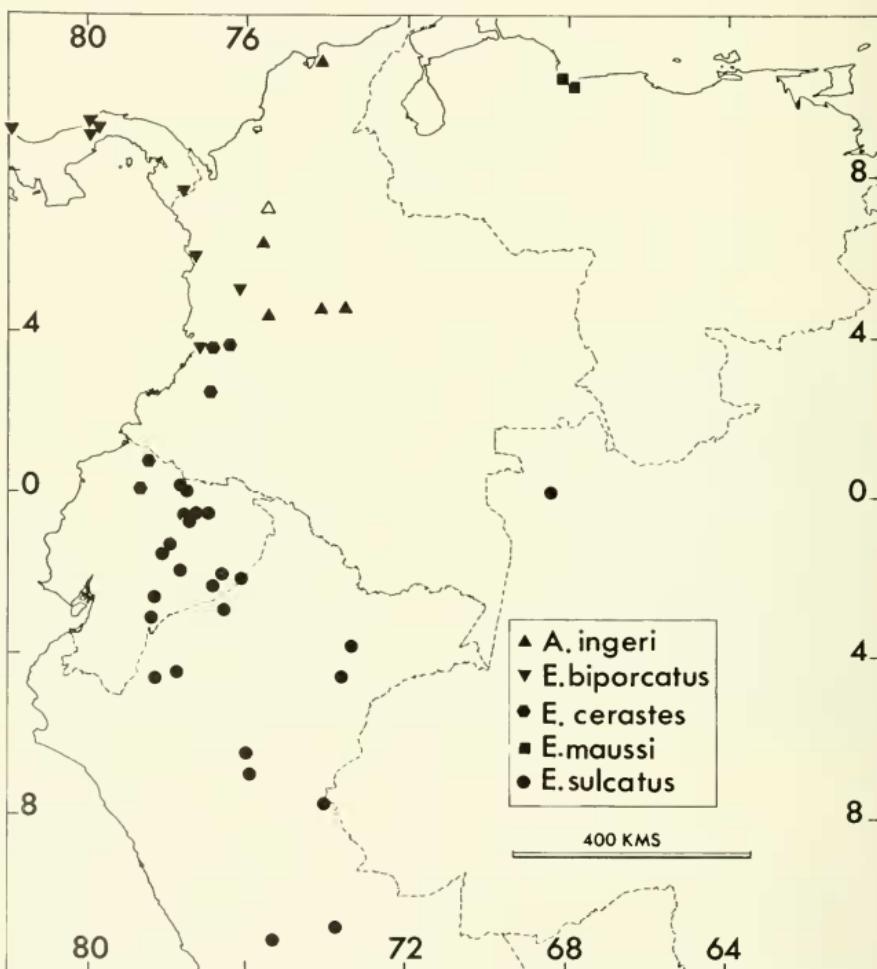


FIG. 10.—Map of northwestern South America showing localities at which *Amblyphryalus ingeri*, *Eleutherodactylus biporcatus*, *E. cerastes*, *E. maussi*, and *E. sulcatus* have been found. Open triangle represents an unverified locality for *A. ingeri*.

from Valdivia, Depto. Antioquia, Colombia (based on FMNH 69742, apparently lost).

Remarks.—In comparison to the adult female, the juveniles are more coarsely tuberculate and have less flaring of the lips. The terminal phalanges of the juvenile frogs bear more pronounced lateral processes than do those of the holotype. The juveniles do not have detectable osteoderms and do not have the lower temporal region occluded by bone. In spite of these differences, which I presume to reflect immaturity, the smaller, juvenile, specimens from Andean Colombia are considered conspecific with the adult female holotype of *A. ingeri*.

Cochran and Goin (1970) referred an adult female eleutherodactyline (FMNH 54591) from the Pacific versant of Colombia to *A. ingeri* and noted certain differences between this specimen and the holotype.

FMNH 54591 is a moderate-sized female (78 mm SVL) of *E. biporcatus* (females 65-110 mm SVL) and certainly not conspecific with the holotype of *Amblyphrynu ingeri*. *A. ingeri* has eight procoelous presacral vertebrae, lacks a vertebral shield, has widely separated cervical cotyles, and a bicondylar sacro-coccygeal articulation. The transverse processes of the anterior presacral vertebrae are somewhat longer than those of the posterior presacral vertebrae and the non-dilated sacral diapophyses (which are deflected posteriorly). The ilia are of the leptodactyline type (Lynch, 1971) in having a dorsolateral ilial prominence (not spike-like) and an ilial crest. The pectoral girdle is arciferal, cartilaginous pre-zonal and post-zonal elements are present, and the clavicles and coracoids are neither slender nor massive and curved.

The most distinctive feature of *A. ingeri* is the absence of an infratemporal fenestrum (Fig. 7). In other leptodactylids having maxillary-squamosal contact (*Caudiverbera*, *Ceratophrys*, *Cyclorana australis*, *Lepidobatrachus*, *Megaelosia*, and *Proceratophrys*) there is a prominent infratemporal fenestrum. The infratemporal fenestrae are small or absent in *Hemiphractus* (Hylidae), *Genyophryne* (microhylidae), and *Ceratobatrachus* (Ranidae), but I know of no other frogs that lack an infratemporal fenestrum.

Amblyphrynu helonotus new species

Fig. 11

Holotype.—BMNH 1970.178, collected at the Río Pitzara, Pichincha Prov., Ecuador, by M. Olalla.

Paratype.—USNM 195784, collected at Mindo, Pichincha Prov., Ecuador, by M. Olalla, 24-31 May 1959.

Diagnosis.—A large eleutherodactyline frog (♀ 60-70 mm SVL) with low, parasagittal cranial crests on the frontoparietals; skull with little exostosis; squamosal not contacting maxilla; prevomerine dentigerous processes arch-like, extending laterally to outer edge of choanae; dorsal skin lacking osteoderms;

skin of dorsum tuberculate bearing large flattened warts; upper eyelid lacking elongate tubercles; no tarsal fold; venter blotched with black or dark brown.

Description.—Head as broad as or broader than body; head wider than long; head width 49.5-51.0% SVL; snout round in dorsal view (Fig. 11), truncate in lateral profile; snout moderately short, eye-nostril distance 93.8-96.1% eye length; canthus rostralis obtuse, not sharp, weakly concave; loreal region flat to weakly concave, sloping gradually to flared lips; interorbital space furrowed, low cranial crests present, not extending onto nasals and not ending in a prominent boss; upper eyelid width 143.4-167.4% IOD; supratympanic fold present, indistinct; tympanum prominent, higher than long, its length 49.7-57.0% eye length, separated from eye by 1½ to 2 times width of tympanum; tongue about as long as wide, weakly notched posteriorly, posterior $\frac{1}{4}$ to $\frac{1}{3}$ not adherent to floor of mouth; choanae small, not concealed by palatal shelf of maxillae; pre vomerine dentigerous processes present, arched, posterior to choanae; each process 3 to 4 times width of a choana; processes narrowly separated, extending to lateral edge of choana.

Skin of dorsal surfaces tuberculate, tubercles heterogeneous (Fig. 11); a pair of indistinct canthal folds present; no enlarged "horn-like" tubercles on eyelids; a pair of λ shaped folds in scapular region; skin of venter coarsely areolate; no dorsolateral folds; discoidal folds not apparent; ulnar tubercles present; two palmar tubercles, outer largest, bifid; supernumerary palmar tubercles prominent, flattened; subarticular tubercles round, simple, non-conical; fingers



FIG. 11.—*Amblyphryalus helonotus* (USNM 195784, paratype).

bearing weak lateral fringes; tips of fingers rounded, lacking pads; thumb longer than second finger.

Heel and inner tarsus lacking tubercles or folds; outer edge of tarsus bearing row of small tubercles; two metatarsal tubercles, inner weakly compressed, twice as long as wide, 2 to 3 times size of rounded, non-conical outer metatarsal tubercle; no supernumerary plantar tubercles; toes bearing lateral fringes but lacking basal webbing; subarticular tubercles round, conical, simple, smaller than those of fingers; tips of toes not expanded, lacking pads.

In preservative, *A. helonotus* is brown above with indefinite black or dark brown markings on the tubercles and folds. No distinct canthal or supratympanic stripes are evident. The face is barred with broad brown labial bars separated by thin cream lines. The venter is cream with dark brown blotches. The throat is dark brown with a few darker spots at the edge of the lip. The undersides of the limbs are dark brown with cream spots. The groin is dark brown and lacks a pattern. The limbs are barred with dark brown; the bars are about as wide as the brown interspaces. The bars on the thigh continue down the anterior face of the thigh and coalesce ventrally

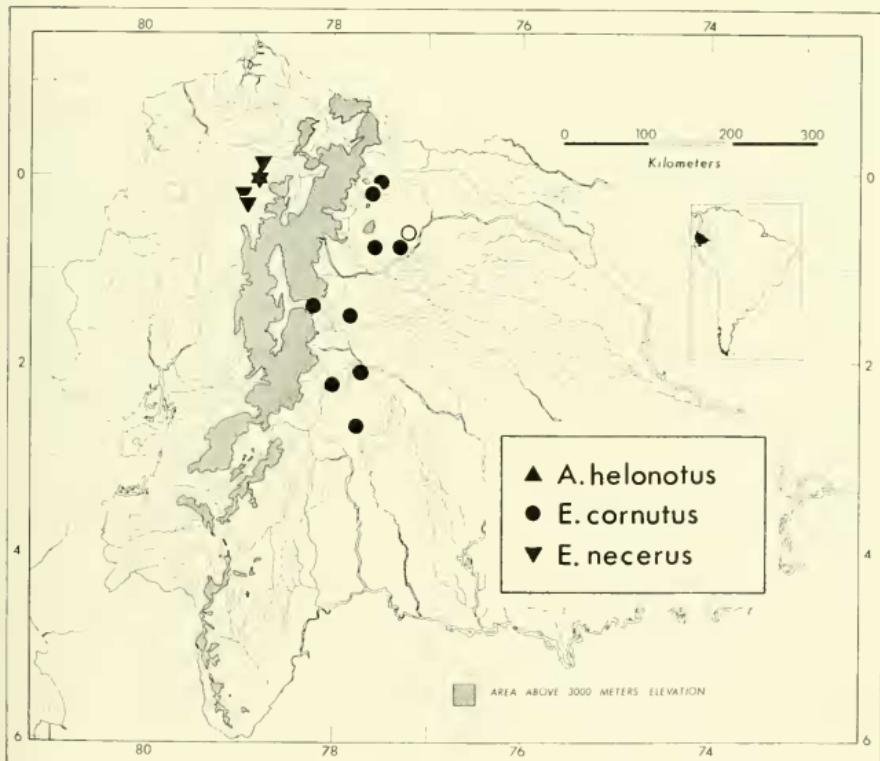


FIG. 12.—Map of Ecuador showing localities at which *Amblyphryalus helonotus*, *Eleutherodactylus cornutus*, and *E. necerus* have been found. Open circle represents a literature record for *E. cornutus*.

with the reticulation on the ventral surfaces of the thighs. The posterior surfaces of the thighs are brown with black reticulations.

Measurements in mm.—The measurements of the type are listed first and the corresponding measurement of the paratype is listed in parentheses. SVL 69.6 (60.6), shank 31.0 (26.6), head width 35.5 (30.0), head length 26.0 (23.4), eyelid width 7.6 (7.2), IOD 5.3 (4.3), tympanum length 3.8 (3.6), eye length 7.6 (6.4), eye-nostril distance 7.4 (6.0).

The holotype is a gravid female (ovarian eggs yellow, 3-4 mm in diameter, heavily convoluted oviducts). The paratype is a young female (ovarian eggs white, $\frac{1}{2}$ -1 mm in diameter, weakly convoluted oviducts).

Etymology.—Greek, *helos* + *notos*, wart + back; in reference to the large warts on the dorsum and flanks.

Distribution.—Known only from the Pacific versant of Ecuador at low and moderate elevations (Fig. 12).

Remarks.—*A. helonotus* differs markedly from *A. ingeri*. Comparable intrageneric variation occurs within *Cyclorana*, *Pyxicephalus*, and *Rhacophorus*. I view the degree of relation between the two species of *Amblyphryalus* as roughly equivalent to that between *Eleutherodactylus biporcatus* and *E. sulcatus*, congeneric, but in different species groups.

Eleutherodactylus Dumeril and Bibron

Diagnosis.—Eleutherodactyline frogs with complex digits (discs present, supported by T-shaped terminal phalanges, at least on toes), teeth on maxillae, premaxillae, and prevomers, and lacking rows of tubercles on the plantar surfaces.

Frogs of this genus are diverse. Most species have narrow heads (HW/SVL:30-42%), lack webbing of the toes, and lack a frontoparietal fontanelle. The various species groups differ in head width (two groups with broad heads, *biporcatus* and *sulcatus*), texture of the venter (smooth vs areolate), finger length (first finger shorter than second vs longer than second), notching of the skin above the finger discs (notched in southeastern Brasilian *Eleutherodactylus*, and some partially studied osteological features (fusion of frontoparietals and proöties, overlap of pterygoid and parasphenoid, size of prevomers, and shape of zygomatic ramus of squamosal). The tympana may be prominent, partially or wholly concealed, or absent. Cranial crests occur sporadically, mostly within the broad-headed groups and in a number of Andean species.

Type-species.—*Hylodes martinicensis* Tschudi, by monotypy.

Content.—Four hundred and thirty names have been proposed; generally 200 to 250 taxa are recognized.

Eleutherodactylus biporcatus (Peters)

Strabomantis biporcatus Peters, 1864:405 [Type-locality—Veragua, Panamá].
Hylodes rugosus Peters, 1874:610 [Type-locality—Chiriquí, Panamá].
Lithodytes megacephalus Cope, 1875:110 [Type-locality—Pico Blanco, Costa Rica, 6000 ft.].
Lithodytes gulosus Cope, 1875:112 [Type-locality—Pico Blanco, Costa Rica, 6000 ft.].
Lithodytes pelvulus Cope, 1877:89 [Type-locality—west coast of Central America].
Hylodes rugosus: Boulenger, 1882:205.
Hylodes gulosus: Boulenger, 1882:211.
Hylodes biporcatus: Boulenger, 1882:220.
Hylodes megacephalus: Brocchi, 1882:57.
Lithodytes florulentus Cope, 1893:336 [Type-locality—Boruca, Costa Rica].
Hylodes florulentus: Gunther, 1901:234.
Eleutherodactylus rugosus: Noble, 1918:329.
Eleutherodactylus biporcatus: Dunn, 1931:410.
Eleutherodactylus florulentus: Taylor, 1952:765.

Diagnosis.—A large *Eleutherodactylus* (adult ♀ ♀ 65-110 mm SVL) with a broad head (HW/SVL = 47.9-54.3%); snout truncate in lateral profile; lips not flared; frontoparietals bear moderate lateral crests terminating posteriorly in large boss, normally not extending onto nasals; tympanum 80.0-89.8% eye length in males, 43.6-50.2% in females; prevomerine dentigerous processes triangular in outline, posteromedial to choanae; males with vocal sac and slits; ulnar tubercles

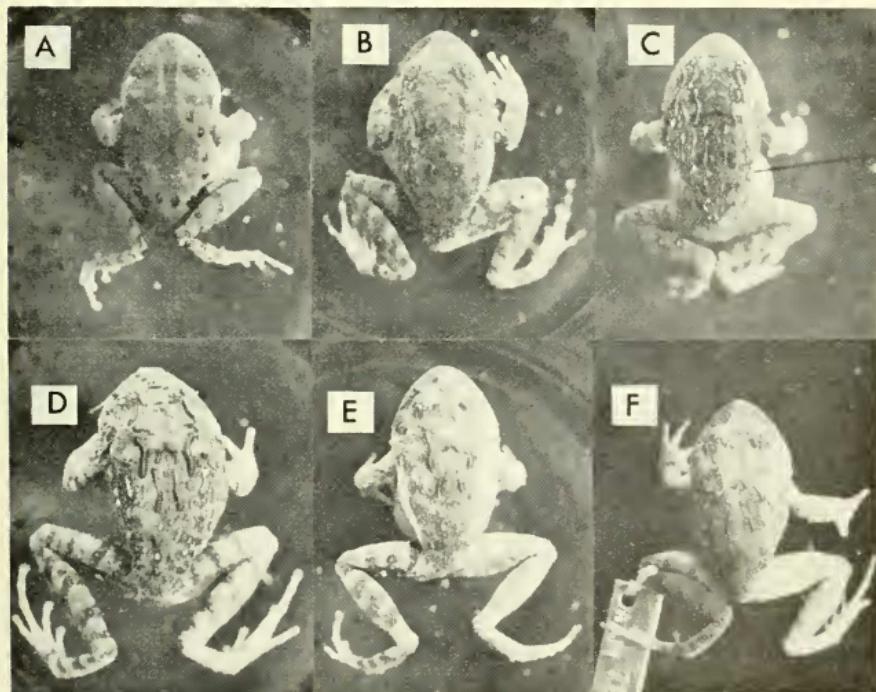


FIG. 13.—Broad-headed *Eleutherodactylus*. (A) *E. biporcatus*, LACM 73154, (B) *E. bufoniformis*, LACM 73248, (C) *E. neckerus*, USNM 195799, (D) *E. cerastes*, USNM 195793, (E) *E. sulcatus*, AMNH 42293, and (F) *E. maussi*, AMNH 70557.

not or only weakly developed; two palmar tubercles, outer largest, bifid; fingers lacking lateral fringes; fingers bearing discs at tips, discs narrow, but broader than fingers; thumb longer than second finger; skin of dorsum moderately tuberculate in young, becoming smooth with scattered tubercles in large adults; upper eyelid tuberculate, no tubercle elongate; skin of venter smooth; tarsus lacking fold along inner margin; inner metatarsal tubercle strongly compressed laterally; outer metatarsal tubercle small and obsolete; plantar surface lacking supernumerary tubercles; toes lacking lateral fringes and basal webbing; toes bearing moderate-sized discs and pads, pads wider than long; posterior surface of thigh black or black with pale areas (posterior extensions of pale areas on dorsal surface of thigh); venter usually reticulated with brown.

Descriptions.—In addition to the original descriptions (Cope, 1875, 1877, 1893, and Peters, 1864, 1874), descriptions are available in Noble (1918) and Taylor (1952, 1955), the latter including illustrations.

Distribution.—Eastern Honduras and Nicaragua through low and moderate elevations to western Colombia (sea-level to about 1000 m).

Remarks.—Jiménez de la Espada (1872) incorrectly referred *Limnophys napaeus* to the synonymy of *E. biporcatus*. The holotype of *napaeus* is lost, but two features cited by Jiménez de la Espada suggest that *napaeus* is a synonym of *cornutus* and not of *biporcatus*: the holotype of *napaeus* was 50 mm SVL, had coarsely tuberculate skin of the dorsum and broad, and arched prevomerine dentigerous processes (Jiménez de la Espada, 1870). Comparable sized *biporcatus* have nearly smooth skin on the dorsum (Fig. 13) and triangular prevomerine processes. Accordingly, *Limnophys napaeus* Jiménez de la Espada is removed from the synonymy of *Eleutherodactylus biporcatus* (Peters).

The specimen (FMNH 54591) reported as *Amblyphryne ingeri* by Cochran and Goin (1970) is a normal female *E. biporcatus* and in no way departs from the diagnosis given above.

Eleutherodactylus bufoniformis (Boulenger)

Hylodes bufoniformis Boulenger 1896:19 [Type-locality—Buenaventura, Valle, Colombia].

Eleutherodactylus bufoniformis: Dunn, 1931:410.

Diagnosis.—A large *Eleutherodactylus* (adult females 52-94 mm SVL) with a broad head (HW/SVL = 44.4-58.2%); snout truncate in lateral profile; frontoparietals bear low parasagittal crests not extending onto nasals; tympanum 2/5 to $\frac{1}{2}$ eye length in females, $\frac{1}{2}$ to $\frac{3}{4}$ eye length in males; prevomerine dentigerous processes triangular in outline, posteromedial to choanae; males with vocal sac and slits; ulnar tubercles present, not enlarged; two palmar tubercles, outer largest, bifid; fingers lacking lateral fringes; digit tips bearing pads and discs, pads wider than finger; thumb longer than second finger, skin of dorsum tuberculate and bearing short ridges in young as well as adult frogs; upper eyelid tuberculate, no tubercles elongate; skin of venter smooth; tarsus lacking inner fold (or having a weak inner tarsal fold); two metatarsal tubercles, inner largest, laterally compressed, outer obscure, small; no supernumerary plantar tubercles; toes bearing lateral fringes and basally webbed (webbing encloses basal sub-

articular tubercles); toes with discs, pads broader than long, larger than those of fingers; posterior surfaces of thighs brown with small cream spots; dark color of lower flanks grades onto venter; venter mottled with brown.

Descriptions.—Boulenger's (1896) brief original description is amplified by Cochran and Goin's (1970).

Distribution.—Low elevations, from extreme western Panamá onto the Chocó lowlands of Colombia.

Eleutherodactylus cerastes new species

Fig. 14

Holotype.—USNM 195785, an immature female, collected at Palma Real, Pichincha Prov., Ecuador, collected June 1955 by M. Olalla.

Paratypes.—KU 144992-93, El Tambo, La Costa, Depto. Cauca, Colombia, 1000 m; KU 144994, El Tambo, Munchique, Depto. Cauca, Colombia, 1000 m; AMNH 88062, 13 km W Dagua, Rio Anchicaya drainage, Valle, Colombia, 850-1200 m; USNM 195786-88, Lita, Rio Mira, Imbabura Prov., Ecuador; USNM 195789-93, Pachijal, Pichincha Prov., Ecuador; USNM 195794, Palma Real, Pichincha Prov., Ecuador.

Referred specimens.—BMNH 1910.7.11.61-62, Pueblo Rico, Depto. Cauca, Colombia, 1580 m; USNM 195795, Lita, Rio Mira, Imbabura Prov., Ecuador; USNM 195796(3), Rio Pitzara, Pichincha Prov., Ecuador; USNM 195797, road from Pacto to Rio Guayllabamba, Pichincha Prov., Ecuador.

Diagnosis.—A large *Eleutherodactylus* (2 adult ♀♀ 46.0-55.8 mm SVL); snout truncate or weakly sloping in lateral profile, lips weakly flared in large adults; frontoparietals bearing low lateral crests, not ending in bosses, not extending onto nasals; tympanum $\frac{1}{3}$ to $\frac{1}{2}$ eye length in females, $\frac{1}{2}$ to $\frac{3}{5}$ eye length in males; prevomers with broad, arched processes, extending laterally to lateral edge of choana; males lacking vocal sac; ulnar tubercles present, not enlarged; two palmar tubercles, outer largest and bifid; fingers lacking lateral fringes; digit tips bearing narrow pads; thumb longer than second finger; skin tuberculate and ridged above in young and adult individuals; upper eyelid bearing elongate tubercle on posterolateral corner; skin of venter smooth; tarsus lacking folds, outer edge bearing row of small tubercles; two metatarsal tubercles, inner laterally compressed, outer small, rounded; no supernumerary plantar tubercles; toes lacking lateral fringes; toes with pads, broader than long, much larger than those of fingers; posterior surfaces of thighs brown with cream spots.

Description of holotype.—Head broader than body, wider than long; head width 45.8% SVL; snout rounded in dorsal view, truncate in lateral profile; snout short, eye-nostral distance 71.2% eye length; canthus rostralis moderately sharp, straight; loreal region concave, sloping abruptly to lips; lips not flared; nostrils directed laterally, weakly protuberant; interorbital space weakly furrowed, edges of frontoparietals bearing low crests; upper eyelid broad, its width 140.6% IOD; supratympanic fold obscure, covering upper edge of tympanum; tympanum prominent, higher than long, its length 37.9% eye length; tympanum separated from eye by distance equal to width of tympanum; skin of head tuberculate; eyelid bearing several large tubercles, one at posterolateral corner greatly elongated; tubercles along canthus forming canthal ridge; tongue about as long as wide, weakly notched posteriorly, posterior $\frac{1}{4}$ free; choanae mod-

erate-sized, not concealed by palatal shelf of maxillae; prevomerine dentigerous processes broad, arched, posterior to choanae, separated medially by $\frac{1}{2}$ choanal width, extending laterally to lateral edge of choanae, bearing a row of 10-12 teeth per process.

Skin of dorsum tuberculate, tubercles heterogeneous, and bearing short paravertebral and dorsolateral ridges, most prominent of which are paravertebral scapular ridges connected by a transverse fold (Fig. 13); tubercles on flanks less heterogeneous than those of dorsum; skin of upper surfaces of limbs bearing heterogeneous tubercles; skin of venter smooth; no dorsolateral folds (other than short ridges); no trace of discoidal folds; posterior surfaces of thighs about vent areolate, a pair of prominent tubercles posterolateral to anus; forearm bearing a series of ulnar tubercles which are not larger than tubercles on upper surface of forearm; two palmar tubercles, outer bifid and larger than inner; no supernumerary palmar tubercles; subarticular tubercles round, low, flat, simple; fingers lacking lateral fringes; digits swollen apically, bearing ill-defined, narrow pads (perhaps due to length of preservation); heel bearing a single, non-elongate tubercle; outer edge of tarsus bearing a series of tubercles, inner edge of tarsus lacking tubercles or folds; two metatarsal tubercles, inner laterally compressed, four times as long as



FIG. 14.—*Eleutherodactylus cerastes* (AMNH 88062). Photo by Charles W. Myers.

wide, about three times size of low, round outer metatarsal tubercle; no supernumerary plantar tubercles; subarticular tubercles longer than wide, non-conical, simple, smaller than those of fingers; toes lacking lateral fringes and webbing; toes bearing dilated pads at tips, pads wider than long, much larger than those of fingers; hind limbs relatively long, heel of adpressed limb reaches to between eye and tip of snout; shank 60.0% SVL.

Coloration in preservative.—The dorsum is brown and the ridges and tubercles dark brown to black; labial bars are present but canthal and supratympanic stripes are not distinct; the limbs are barred with dark brown, the dark bars are narrower than the brown interspaces. The groin, lower flanks, and anteroventral surfaces of the thighs are boldly marked with brown bars and spots on a pale cream background; the posterior surfaces of the thighs are dark brown with cream spots. The venter and undersides of the limbs are cream with moderate to intense brown motting and reticulation. The throat is brown punctated with cream.

Variation.—Males lack vocal sacs and slits and tend to have larger ears than do females. Other than the variation in ear size, the proportions do not suggest sexual dimorphism. Males are smaller than females and within my samples the only mature females are 46 and 55.8 mm SVL. A female (USNM 195785, the holotype) is an immature female 46.7 mm SVL. The immature females (small eggs and weakly convoluted oviducts) range in size from 35-46.7 mm SVL. Females with straight oviducts are 32.7 mm SVL or smaller.

The three adult or subadult Colombian specimens (KU 144992-94) have weakly-flared lips and weakly-sloping snouts (in lateral profile). They also differ from the Ecuadorian specimens in having more rounded warts on the body. These differences might be simply geographic variation, but the less "sharp" warts may be due to the vicissitudes of preservation. A juvenile from Colombia also has more rounded warts (Fig. 14).

Measurements of the holotype.—In mm, SVL 46.7, shank 28.0, head width 21.4, head length 16.3, eyelid width 4.8, IOD 3.4, tympanum length 2.5, eye length 6.6, eye-nostiril distance 4.7

Etymology.—Greek, *kerastes*, horned: in reference to the eyelid tubercle.

Distribution.—Known from low to moderate elevations (ca. 500-1580 m) along the Pacific versant of Colombia and Ecuador (Fig. 10).

Remarks.—*E. cerastes* appears closely allied to *E. biporcatus*, distributed to the north, and to *E. cornutus*, found at comparable (or slightly higher) elevations on the Amazonian versant of the Ecuadorian Andes. The three are readily distinguished, even as juveniles, in that *E. biporcatus* lacks elongate eyelid tubercles (present in *cerastes* and *cornutus*) and *E. cornutus* has a prominent inner tarsal

fold and lateral fringes on the toes (lacking in *biporcatus* and *cerastes*).

Eleutherodactylus cornutus (Jiménez de la Espada)

Limnophys cornutus: Jiménez de la Espada, 1870:60 [Type-locality—Río Suno, San José de Motí, Napo Prov., Ecuador].

Limnophys napaeus: Jiménez de la Espada, 1870:60 [Type-locality—Río Suno, San José de Motí, Napo Prov., Ecuador]. *New synonymy*.

Strabomantis cornutus: Jiménez de la Espada, 1872:85.

Hylodes cornutus: Boulenger, 1882:220.

Ctenocranius cornutus: Melin, 1941:49.

Lithodytes cornutus (part): Anderson, 1945:45.

Eleutherodactylus cornutus cornutus (part): Rivero, 1961:55.

Eleutherodactylus cornutus: Gorham, 1966:66.

Diagnosis.—A large *Eleutherodactylus* (immature ♀ 54.0 mm SVL) with a broad head (HW/SVL = 48.8-56.4%); snout truncate in lateral profile; frontoparietals bearing prominent lateral crests ending in elevated bosses; crests not extending onto nasals; tympanum prominent, 2/5 to $\frac{1}{3}$ eye length; preovomerine dentigerous processes arch-like, extending laterally to outer edge of choanae; male lacking vocal sac and slits; ulnar tubercles prominent; two palmar tubercles, outer largest, bifid; fingers bearing weak lateral fringes; tips of fingers bearing narrow discs; first finger longer than second; skin of dorsum coarsely tuberculate; H shaped series of folds in center of back; posterolateral corner of upper eyelid bearing one or two elongated tubercles; skin of venter smooth; tarsus bearing fold along inner margin; two metatarsal tubercles, inner larger, not compressed, outer small but easily detected; no supernumerary plantar tubercles; toes bearing lateral fringes without basal webbing; toes bearing dilated discs, discs larger than those of fingers; posterior surface of thighs black with cream flecks; venter brown with diffuse white blotches.

Description.—(Also see Fig. 15). The only descriptions of this species are the brief descriptions of Jiménez de la Espada (1870). To prevent further confusion, such as that of Boulenger (1882) and Rivero (1961), the species is here redescribed on the basis of two young males (BMNH 1913.11.1.57, KU 143350), a young female (KU 123448), and 36 juveniles. Head as broad as or broader than body, wider than long; head width 48.8-56.4% ($\bar{x} = 52.2$) SVL; snout

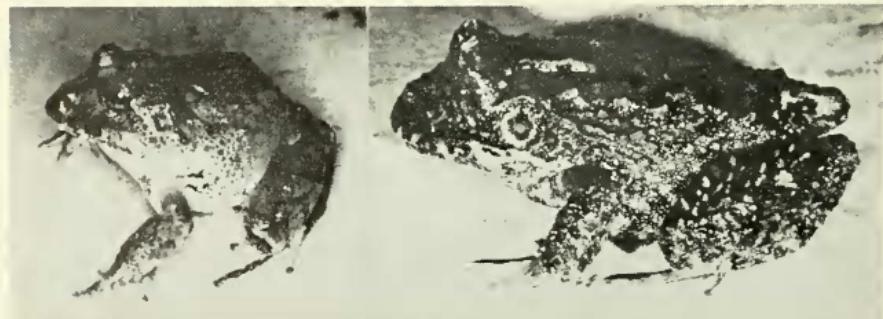


FIG. 15.—*Eleutherodactylus sulcatus* (left, KU 143350) and *E. cornutus* (right, KU 123586). Photos by William E. Duellman.

round in dorsal view, short and truncate in lateral profile; eye length greater than eye-nostril distance; canthus rostralis sharp, concave, sloping gradually to lips, lips weakly flared; nostrils protuberant, directed laterally; tip of snout not bearing ridge or proboscis, not extending much beyond lower jaw; interorbital region concave, edges of frontoparietals enlarged; upper eyelid tuberculate, tubercles near posterolateral corner of eyelid greatly elongated (Fig. 1); cranial crests ending in bosses posteromedial to eyes, least prominent anteriorly; tympanum prominent, slightly higher than long; tympanic region not vertical, weakly oblique due to flaring of maxillary arch; tympanum length 39.5-54.3% eye length in specimens 20-27 mm SVL, 55.5, 60.3, 66.7% in specimens 35.5, 43.0, and 54.0 mm SVL; supratympanic fold tuberculate; edge of lower jaw bearing a row of prominent tubercles; tongue small, round, weakly notched behind, posterior edge free; choanae small, teardrop-shaped, well within border of jaw when roof of mouth viewed from directly above, separated medially by distance equal to 6 times width of choana; prevomerine teeth in transverse series on prominent, triangular processes lying posterior to choanae; 8-9 teeth per process, processes in median contact; male lacking vocal sac and slits.

Skin of dorsum bearing numerous tubercles and ridges in apparently constant though complex pattern; prominent interorbital tubercle; ciliary ridges lateral to cranial crests; dermal ridges extend posteriorly from terminis of cranial crest as scapular folds with a cross bar in scapular region; dorsolateral region bearing rows of tubercles; center of back from scapular "H" to vent bearing numerous short folds; limbs bearing oblique bars of tuberculated ridges (Fig. 16); ulnar region bearing series of prominent flap-like tubercles; heel tuberculate but no tubercle elongated; skin of throat, venter, underside of limbs smooth except just below vent where skin is areolate; flanks areolate; discoidal fold present, ending anterior to groin; shank 54.7-63.0% ($\bar{x} = 57.4$) SVL.

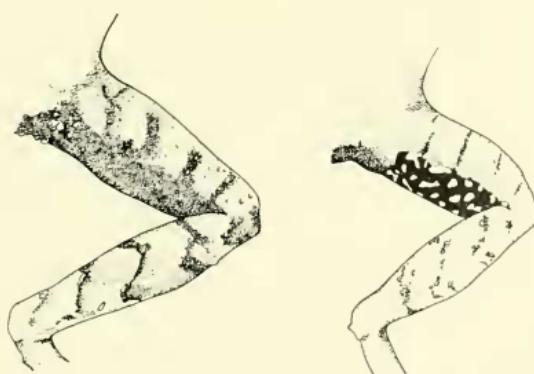


FIG. 16.—Color patterns of hind limbs of *Eleutherodactylus cornutus* (left, KU 123448) and *E. sulcatus* (right, KU 123586).

Two palmar tubercles, outer bilobed (fused median and outer); supernumerary palmar tubercles at base of digits, not extending onto digits; subarticular tubercles round, simple, weakly conical; fingers bearing thin lateral fringes; digits bearing pads with circumferential grooves, pads less than $1\frac{1}{2}$ times digit width below pad; first finger longer than second.

Inner edge of tarsus bearing distinct fold $\frac{1}{2}$ tarsus length; outer edge of tarsus bearing row of conical tubercles; inner metatarsal tubercle elongate, not compressed; outer metatarsal tubercle prominent, longer than wide, not elevated, $\frac{2}{3}$ size of inner; plantar surface bearing a few minute supernumerary tubercles; subarticular tubercles like those of fingers but smaller; toes bearing lateral fringe and basal web, web not enclosing basal subarticular tubercle on any toe; toes bearing pads, pads $1\frac{1}{2}$ times width of digit below pad; outer edge of foot and fifth toe bearing tuberculate ridge; third toe longer than fifth toe.

Coloration.—In preservative, brown with reddish-brown ridges and warts edged with black; limbs barred with narrow black bars about one-fourth width of brown interspaces; labial barring dark brown to black; posterior surface of thigh black with silvery or golden flecks (Fig. 16); venter heavily reticulated with brown on a white ground color; throat brown with fine cream mottling; undersides of limbs brown with diffuse white blotching; flanks brown with diffuse white spots.

In life, *E. cornutus* was described as follows (W. E. Duellman, field notes): "Dorsum dark dull reddish brown; posterior surface of thigh black with bluish-white flecks. Venter dark brown and grayish-white. Throat reddish-brown. Feet orange tan. Iris dull bronze with black reticulation and a median horizontal brown streak" (20 October 1971). "dorsum dull olive-brown with black and reddish-brown markings. Groin and ventral surfaces of legs black and white. Throat and belly brown and white. Posterior surface of thigh black with small white flecks. Iris tan with brown triangles. Tongue bright yellow." (3 August 1968).

Distribution.—Known only from moderate elevations (500-2000 m) along the eastern base of the Ecuadorian Andes (Fig. 12).

Remarks.—Authors referring to *E. cornutus* fall into two categories, those citing the name without specimens and those applying the name to other species. Dunn (1944) applied the name *cornutus* to what has become the holotype of *Amblyphryalus ingeri*. Andersson (1945), Cochran and Goin (1970), and Rivero (1961) applied the name *cornutus* to specimens of *E. sulcatus*. Boulenger (1882), Cochran and Goin (1970), and probably Peracca (1914), used the name for young *Amblyphryalus ingeri*.

I regard *Limnophys napaeus* Jiménez de la Espada as a synonym of *E. cornutus*. Jiménez de la Espada (1870) distinguished *cornutus* and *napaeus* on the basis of tongue shape, the narrow separation of

the prevomerine teeth, the longer eye tubercle of *cornutus*, and minor differences in coloration. Both were included in the genus *Limnophys*, which was characterized in part by the tuberculate eyelid. Examination of the type of *napaeus* could resolve the question of its identity (Jiménez de la Espada published several illustrations of *cornutus* in his 1875 work), but the types of both species are evidently lost (William E. Duellman was unable to find them when he studied Jiménez de la Espada's material in 1969). Jiménez de la Espada (1872) placed *napaeus* in the synonymy of *biporcatus*, and this action was followed by all subsequent authors. Geographically, it seems reasonable to argue that *cornutus* and *napaeus* are identical, especially in view of Jiménez de la Espada's (1870) description in which the skin of the dorsum was characterized as warty for the 50 mm SVL type of *napaeus*. Comparable sized *biporcatus* would be characterized as having smooth skin with scattered warts. Additionally, the arched prevomerine processes of *napaeus* agree with *cornutus* but not *biporcatus* (prevomerine processes triangular in outline).

Eleutherodactylus maussi (Boettger)

Hylodes maussi Boettger 1893:99 [Type-locality.—Puerto Cabello, Estado Carabobo, Venezuela].

Eleutherodactylus maussi: Gines 1959:112.

Eleutherodactylus cornutus maussi: Rivero 1961:54.

Diagnosis.—A large *Eleutherodactylus* (adult ♀ ♀ 56-70 mm SVL) with a broad head (HW/SVL = 44.3-54.9%); snout strongly sloping in lateral profile; lips flared in adults (flaring increases with size); frontoparietals bearing lateral crests, crests ending in moderate boss; crests not extending onto nasals; tympanum prominent, 60-87% eye length; prevomerine dentigerous processes arch-like, extending laterally to outer edge of choanae; males with vocal sac and slits; ulnar tubercles prominent; fingers bearing weak lateral fringes; fingers bearing narrow discs at tips, first finger longer than second; skin of dorsum tuberculate; eyelid tuberculate, no tubercle elongate; skin of venter coarsely areolate; tarsus bearing fold along inner margin; two metatarsal tubercles, inner larger than outer, not compressed, outer prominent; plantar surface bearing numerous supernumerary tubercles; toes bearing lateral fringes but no basal webbing; toes bearing comparatively broad discs; posterior surface of thighs brown with cream flecks; venter cream.

Descriptions.—Boettger (1893) and Nieden (1923) provide brief descriptions; that of Rivero (1961) is more complete.

Distribution.—Known only from the Coastal Range of Venezuela (Fig. 10).

Remarks.—*E. maussi* is certainly not conspecific with *E. cornutus*, but its relationship to *E. sulcatus* is close. The structural differences between *maussi* and *sulcatus* are more extensive than Rivero (1961) realized. Heatwole (1962) reported on several aspects of the biology of *maussi*; comparable information is not available for any of the other broad-headed eleutherodactylines.

Eleutherodactylus necerus new species

Holotype.—USNM 195798, an adult female collected at Mindo, Pichincha Prov., Ecuador.

Paratype.—USNM 195799, a juvenile female collected at the Rio Lelia, a tributary of the Rio Toachi, Pichincha Prov., Ecuador.

Referred specimens.—Two juveniles: USNM 195852, Rio Blanco, near mouth of Rio Yambi, Pichincha Prov., Ecuador, 700 m; USNM 195851, road from Pacto to Rio Guayllabamba, Pichincha, Ecuador.

Diagnosis.—A large *Eleutherodactylus* (adult female 93.3 mm SVL); snout truncate in lateral profile; lips not flared; frontoparietals bearing low parasagittal crests not ending in bosses, not extending onto nasals; tympanum $\frac{1}{2}$ to $\frac{2}{5}$ eye length in females; prevomers with broad, arched processes (adult only), extending laterally to middle of choana (not triangular); ulnar tubercles present, not enlarged; two palmar tubercles, outer largest, bifid; fingers lacking lateral fringes; digit tips bearing discs, narrow; thumb longer than second finger; skin tuberculate and ridged above in young and adult frogs; upper eyelid tubercular, no tubercle elongate; skin of venter smooth; tarsus lacking tubercles or folds; two metatarsal tubercles, inner laterally compressed, outer obsolete, no supernumerary plantar tubercles; toes bearing lateral fringes, no basal webbing; toes with discs (broader than long), toe pads larger than those of fingers; posterior surfaces of thighs black with large cream spots; venter cream without brown mottling.

Description of holotype.—Head as broad as body; broader than long; head width 46.2% SVL; snout rounded in dorsal view, truncate in lateral profile; snout short, eye-nostil distance 78.4% eye length; canthus rostralis obtuse, concave; loreal region concave, sloping gradually to flared lips; nostrils directed laterally, weakly protuberant; interorbital region furrowed, narrow; upper eyelid 146.3% IOD; supratympanic fold present, not prominent, obscuring upper edge of tympanum; tympanum higher than long, its length 38.8% that of eye; tympanum separated from eye by 1½-2 times width of tympanum; skin of head smooth with numerous large warts; warts numerous and prominent on eyelid, none elongated (Fig. 13); canthal folds present; tongue as long as wide, weakly notched posteriorly, posterior $\frac{1}{4}$ free; choanae large, not concealed by palatal shelf of maxillae; prevomerine dentigerous processes present, arched, posteromedial to choanae; processes in median contact, extending laterally to middle of choana; 13-16 teeth per process in an oblique row.

Skin of dorsum and limbs bearing numerous small tubercles; dorsum bearing numerous short ridges, none elongate; transverse fold in scapular region; flanks not greatly tuberculate; skin of concealed surfaces and venter smooth; no enlarged post-anal tubercles.

Forearm not bearing distinct ulnar tubercles or folds; two palmar tubercles, outer largest, bifid; no supernumerary palmar tubercles; subarticular tubercles round, non-conical, (not flattened) simple; fingers lacking lateral fringes except for a faint fringe on inner edge of second finger; tips of fingers swollen, bearing narrow, obscure discs; first finger much longer than second (tip of adpressed second finger reaches base of pad of thumb).

Heel and tarsus lacking tubercles or folds; two metatarsal tubercles, inner laterally compressed, 4 times as long as wide, outer obscure, 1/6 to 1/7 the size of inner metatarsal tubercle; no supernumerary plantar tubercles; subarticular tubercles longer than wide, non-conical, simple; toes bearing thin lateral fringes and brief basal webbing (webbing does not encompass the proximal base of the basal subarticular tubercle); toes bearing discs, pads wider than long, much larger than those of fingers.

Coloration (in preservative).—Dorsum medium to dark brown with indefinite darker brown spots and blotches; limbs barred with dark brown, bars about equal (or slightly narrower) in width to interspaces; venter cream or white except for some dark brown spots at edge of lower jaw and at base of arm; lower flanks bearing heavy black reticulation continuing posteriorly onto anterior surfaces of thigh, shank, and tarsus; posterior surfaces of thigh black with large cream spots; lower edge of dorsal pigmentation on concealed thighs and shanks is marked by heavy black reticulation which does not grade into white venter.

Variation.—The paratype is a juvenile female (30.2 mm SVL). It differs from the holotype in having non-flared lips, heterogeneous warts on the dorsum, and in having a series of small tubercles along the outer edge of the tarsus.

Measurements in mm.—Data for the holotype are presented first followed by the corresponding data for the paratype. SVL 93.3 (30.2), shank 52.8 (17.2), head width 43.1 (15.0), head length — (12.5), eyelid width 9.0 (—), interorbital distance 6.2 (—), tympanum length 4.5 (1.7), eye length 11.6 (4.6), eye-nostril distance 9.1 (3.4).

Etymology.—Greek, *nekeros*, hornless, in reference to the absence of an elongated tubercle on the eyelid.

Distribution.—Known only from moderate elevations on the Pacific versant of Ecuador (Fig. 12).

Remarks.—*E. neckerus* is most similar to *E. bufoniformis* but differs in not having toe web enclosing the basal subarticular toe tubercles and in having arched rather than triangular prevomerine dentigerous processes. The two species are dichopatrically distributed in the Chocoan region.

Eleutherodactylus sulcatus (Cope)

Hylobates sulcatus Cope, 1874:126 [Type-locality—Nauta, Depto. Loreto, Peru].

Hylobates macrocephalus Peracca, 1904:29 [Type-locality—Valle Santiago, Morono-Santiago Prov., Ecuador]. [new synonymy].

Ctenocraunus koki Melin, 1941:45, fig. 27. [Type-locality—Taracuá, Rio Uau-pés, Estado Amazonas, Brasil.] [new synonymy].

Lithodytes cornutus (part): Andersson, 1945:45.

Eleutherodactylus macrocephalus: Peters, 1955:348.

Eleutherodactylus cornutus cornutus (part): Rivero, 1961:55.

[*Eleutherodactylus*] *koki*: Myers, 1962:198.

Eleutherodactylus sulcatus: Gorham, 1966:103.

Diagnosis.—A large *Eleutherodactylus* (adult females 28.8-59.7 mm SVL) with broad heads (HW/SVL = 45.6-53.3%); snout sloping in lateral profile; lips flared in adults (degree of flaring increases ontogenetically); frontoparietals bearing prominent lateral crests, crests ending in a boss, crests usually not extending onto nasals; tympanum $\frac{1}{2}$ eye length in males, $\frac{1}{2}$ to $\frac{2}{3}$ eye length in females; prevomers with broad, arched processes, extending laterally to lateral edges of choanae; males lacking vocal sac and slits; ulnar tubercles present, prominent; two palmar tubercles, outer largest, bifid; fingers with weak lateral fringes; digit tips of fingers lacking discs; thumb longer than second finger; skin tuberculate above in young and adult individuals; upper eyelid tuberculate, occasionally an elongate tubercle present; skin of venter coarsely areolate; tarsus bearing fold along inner edge; two metatarsal tubercles, inner not greatly compressed, outer smaller, prominent; plantar surfaces bearing numerous supernumerary tubercles; toes bearing lateral fringes; tips of toes bearing discs; pads wider than long; posterior surface of thighs black with cream spots (Fig. 16); venter cream with some brown suffusion on throat and chest. The throat of males is darker than that of females.

Descriptions.—(Fig. 13); Andersson (1945), Cochran and Goin (1970), Cope (1874), Melin (1941), and Peracca (1904). Those by Melin and Peracca are descriptions of immature specimens. The small size of males is striking; males have most of the ventral surface washed with dull brown. Comparable sized (as well as adult) females are cream below. The males examined do not have vocal slits or a vocal sac. In life, *E. sulcatus* was described as "dull tan with brown markings dorsally; posterior surface of thigh black with pale yellow flecks; venter creamy gray; iris dull gray." (W. E. Duellman field notes).

Distribution.—Upper Amazon basin (150-950 m) in western Brasil, eastern Ecuador, and eastern Peru (Fig. 10). Although no specimens are known, *E. sulcatus* must also occur in southeastern Colombia.

Remarks.—The type specimens of *koki*, *macrocephalus*, and *sulcatus* agree in color pattern, snout shape, proportions, and tuberculation of the body, limbs, and hands and feet. Perraca (1904) separated *macrocephalus* and *sulcatus* on the basis of the former lacking frontoparietal crests and the associated interorbital furrow and because he thought *macrocephalus* differed from *sulcatus* in having an oblique orientation of the tympanum instead of a vertical orientation. The lectotype (here designated) of *macrocephalus* (the larger of the two individuals included in MZS 2930) is 35 mm in snout-vent length and that of *sulcatus* 47 mm SVL. The holotype of *sulcatus* does not have a vertically oriented tympanum as reported by Peracca (1904); all moderate to large-sized individuals of *sulcatus* have flared maxillae and hence an oblique orientation of the tympanum. As Peracca reported, the holotype of *macrocephalus* does not have frontoparietal crests and thus is not different from most individuals of its size class included in *sulcatus*. The fronto-

parietal crests enlarge with increase in body size and their development occurs at smaller SVL in females than in males. The holotype of *sulcatus* is a female with exceptionally well developed crests compared to larger individuals and appears to represent an abnormal individual.

Melin (1941) did not attempt to distinguish *koki* from *sulcatus* and did not cite distinguishing features. The holotype of *koki* is a juvenile and does not differ from immature specimens of *sulcatus*. In the absence of distinguishing features (other than those unique to frontoparietal crest hypertrophy in the holotype of *sulcatus*), *Ctenocranius koki* Melin and *Hylodes macrocephalus* Peracca are placed in the synonymy of *Hylodes sulcatus* Cope.

Rivero's (1961) *Eleutherodactylus cornutus cornutus* is the same as *E. sulcatus*. I agree with Rivero that the Coastal Range population of the *sulcatus* group (*E. maussi*) is related to an Upper Amazon population (*E. sulcatus*) but refrain from asserting a subspecific relationship in the absence of any evidence of integration. The features distinguishing the two populations are more numerous than those cited by Rivero.

There are several literature records of *E. cornutus* from Andean Colombia (Boulenger, 1882; Cochran and Goin, 1970; Dunn, 1944; and Peracca, 1914). All are apparently based on *Amblyphryalus ingeri*.

RELATIONSHIPS OF THE BROAD-HEADED ELEUTHERODACTYLINES

Based on prior experience (subjective systematics) *E. biporcatus*, *E. bufoniformis*, *E. cerastes*, *E. cornutus*, and *E. nigerus* seem to form a closely-knit group of species, and *E. maussi* and *E. sulcatus* form a second group. Within the first group, *E. bufoniformis* and *E. nigerus* combine as an allopatric species-pair, and *E. biporcatus*, *E. cerastes*, and *E. cornutus* constitute a second Artenkreis. A third group of species includes *A. helonotus* and *A. ingeri* but the closeness of their relationships is comparable to that between *E. cornutus* and *E. sulcatus*, i.e., different species-groups within a genus.

The question of relationships within the complex of broad-headed eleutherodactylines is of less interest than that of the relationships of members of this complex to frogs having "normal-width" heads. The commonality of superficial character-states between *E. bufoniformis*, *E. biporcatus*, and a number of species in the *fitzingeri-longirostris* group has long been recognized. Cochran and Goin (1970) included *E. bufoniformis* in their Group I (= *fitzingeri* group auctorum). *E. anomalus*, *E. fleischmanni*, and *E. taurus* are species of the *E. fitzingeri* group that closely resemble *E. bufoniformis* but have narrow heads and little or no development of cranial crests. These species, in turn, grade into the "smooth-skinned" members of Group I (e.g., *E. achatinus*, *E. conspicillatus*,

E. fitzingeri, *E. w-nigrum* among others). The relationships of *Amblyphrynu*s are problematic. It might be a remnant of a "proto-*Eleutherodactylus*" stock that had not acquired digital discs or the absence of digital discs in *Amblyphrynu*s might be secondary. Discovery that the terminal phalanges have short lateral projections does not resolve the question.

In an attempt to test my subjective concept of relationships, I re-evaluated the data from the viewpoint of cladistics and constructed a cladogram following the methods described by Camin and Sokal (1965). The cladistic methodology results in a more objective base from which taxonomic decisions may be made.

The greatest measure of subjectivity in a cladistic analysis is the determination of direction of change among character-states. Direction of change for the majority of traits listed below is based on two assumptions: (1) Primitive proto-*Eleutherodactylus* had a morphology not unlike that exhibited by the extant genera *Hylactophryne* and *Ischnocnema*. The only change necessary to convert these frogs into *Eleutherodactylus* is the acquisition of digital discs. (2) Character-states sporadic in occurrence among frogs are more likely to be derived than primitive (e.g., eyelid tubercles, tarsal fold, supernumerary plantar tubercles, flared lips, cranial crests, and broad heads).

On the basis of both assumptions, characteristic 5 is miscoded below. My initial cladistic run was made with the trait coded in the reverse of that listed below. The result was a lack of compatibilities with other traits and a high number of extra evolutionary steps. I recoded the trait (as listed below) and, with the discovery of compatibilities and a reduction in the number of extra steps, treated the feature as miscoded. Characteristic 6 is miscoded on the basis of assumption 1 (all five species of *Hylactophryne* and *Ischnocnema* have supernumerary plantar tubercles); however, on the basis of assumption 2, it is correctly coded (supernumerary plantar tubercles are sporadic in occurrence). Fewer evolutionary steps are required when characteristic 6 is coded as listed below than when coded in the reverse.

The characteristics (and their coding) used in the analysis are as follows:

1. Prevomerine processes; triangular processes (0) are considered primitive to arched processes (1).
2. Texture of skin on venter; smooth venters (0) are considered primitive to coarsely areolate venters (1).
3. Eyelid tubercles; the presence of elongated tubercles on the eyelid (1) is coded as derived, their absence as primitive (0).
4. Tarsal fold; the presence of an inner tarsal fold is coded as derived (1).
5. Digital discs; the presence of discs on all fingers and toes is

coded as primitive (0), the absence of discs on the fingers as derived (1), and the absence of discs on all digits as further derived (2).

6. Supernumerary plantar tubercles; the presence of such tubercles in adults is coded as derived (1).
7. Lateral fringes on the toes; the absence of such fringes is coded as primitive (0), their presence as derived (1), and their presence with basal (or more) webbing of the toes as further derived (2).
8. Flared lips; flared lips are coded as derived (1).
9. Snout shape; truncate snouts are coded as primitive (0), sloping snouts as derived (1).
10. Cranial crests; the presence of crests on the frontoparietals is coded as derived (1).
11. Head width; narrow heads ($HW < 45\% SVL$) are coded as primitive (0), broad heads ($HW > 45\% SVL$) as derived (1).
12. Snout length; eye-nostir distance $<$ eye length is coded as primitive (0), eye-nostir $>$ eye length (long snout) is coded as derived (1).

The twelve characteristics and their 26 character-states were tabulated for each of twelve species of eleutherodactylines (three of which are "narrow headed" taxa). The species are as follows: 1. *Amblyphryalus ingeri*, 2. *A. helonotus*, 3. *Eleutherodactylus sulkatus*, 4. *E. maussi*, 5. *E. cornutus*, 6. *E. cerastes*, 7. *E. biporcatus*, 8. *E. bufoniformis*, 9. *E. necerus*, 10. *E. anomalus*, 11. *E. fitzingeri*, and 12. *E. conspiciollatus*. A compatibility matrix (Table 1) was ob-

TABLE 1.—COMPATIBILITY MATRIX (12 CHARACTERISTICS AND 12 ELEUTHERODACTYLINE FROG SPECIES); THE PATTERNS (COLUMNS) ARE THE NUMBERS OF EXTRA STEPS FROM EACH OF 12 PATTERN TABLES.

Characteristics	Patterns												Compati- bilities	Extra steps
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII		
1.	X	1	1	1	2	1	1	1	1	0	0	0	3	9
2.	1	X	1	1	1	1	0	1	1	0	0	0	4	7
3.	1	1	X	1	1	0	1	0	0	0	0	0	6	5
4.	1	1	1	X	2	1	0	1	1	0	0	0	4	8
5.	2	0	2	2	X	1	0	1	1	0	0	0	5	9
6.	0	0	0	0	1	X	0	0	0	0	0	0	10	1
7.	1	1	1	1	1	1	X	1	1	2	2	2	0	14
8.	0	0	0	0	1	0	0	X	0	0	0	0	10	1
9.	0	0	0	0	1	0	0	0	X	0	0	0	10	1
10.	1	1	1	1	1	1	2	1	1	X	0	0	2	10
11.	1	1	1	1	1	1	2	1	1	0	X	0	2	10
12.	0	0	0	0	0	0	1	0	0	0	0	X	10	1
Compatibilities	4	5	4	4	1	4	6	4	4	10	10	10	66	---
Extra steps	8	6	8	8	12	7	7	7	7	2	2	2	---	76

tained from the 12 pattern tables (one for each characteristic) and a cladogram of 22 steps was constructed by the monothetic method (Camin and Sokal, 1965). Were all characteristics parsimonious with one another, a cladogram of 14 steps would result. No trait was weighted more than another except by virtue of selection (Inger, 1958).

The resultant cladogram (Fig. 17) may be altered by adopting the equally parsimonious subcladograms (A' and B'). Choice of the alternative subcladograms will reflect characteristic bias on the part of the investigator. My biases are indicated by my choice of subcladogram A over A' and B over B'. A further bias is revealed with the assignment of taxonomic status to various clusters of OTUs. I have grouped OTUs 1 and 2 as the genus *Amblyphrynu*s (primary trait—absence of digital discs) and assigned OTUs 3-12 to *Eleutherodactylus*. The species of *Eleutherodactylus* are further arranged into three clusters: OTUs 3 and 4 as the *E. sulcatus* group, OTUs 5-9 as the *E. biporcatus* group, and OTUs 10-12 as part of the *E. fitzingeri* group. Many more taxa belong to the *E. fitzingeri* group (*E. longirostris* group *auccitorum*) than the three species listed above but I know of no other nominate taxa (other than those assigned to synonymies herein) of the *E. biporcatus*, *E. sulcatus* groups or of the genus *Amblyphrynu*s.

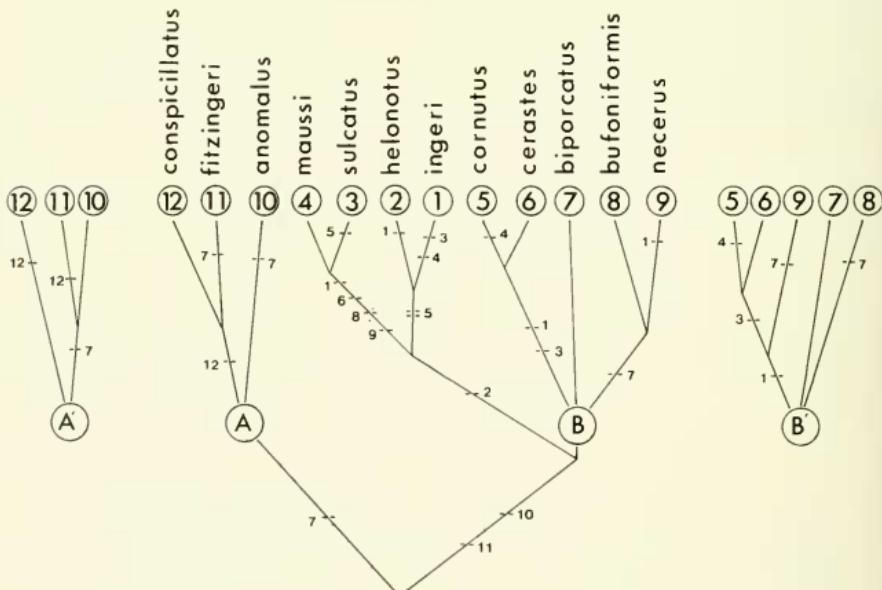


FIG. 17.—Cladogram depicting relationships among the broad-headed eleutherodactylines and three narrow-headed *Eleutherodactylus*. Subcladograms A' and B' may be substituted at nodes A and B, respectively, resulting in equally parsimonious cladograms. Character-state shifts are indicated by horizontal bars and are numbered (see list of characteristics).

DISCUSSION

The presence of simple digits (no pads or discs) in *Amblyphrynnus* led me to believe that these frogs were more primitive than *Eleutherodactylus* (discs uniform). It is difficult to distinguish between primitively simple digits and secondarily simple digits on the basis of digits alone. By not weighing traits and by simultaneously considering several traits I hoped that Camin and Sokal's technique would allow resolution of this dilemma. When I first tabulated the character-tables and compatibility matrix, I coded characteristic 5 in reverse to that given above (first coding: no discs—0, discs on toes only—1, discs on all digits—2). The resulting compatibility matrix with the lack of compatibilities and the high number of extra evolutionary steps suggested miscoding of this trait. In the cladogram constructed from this initial analysis, the species of *Amblyphrynnus* remained derived taxa rather than primitive taxa in spite of an apparent miscoding of trait 5. I am now convinced that the simple digits of *Amblyphrynnus* are secondarily simple as opposed to the primitively simple digits in many telmatobiine leptodactylids. I interpret the secondarily simple digits as an adaptation to terrestrial existence. For the most part, the species of the *E. fitzingeri* group are found on low vegetation in the herbaceous layer of the forests (within 1-2 m of the ground). The broad-headed taxa are found on the forest floor (in litter by day; actively hopping about by night).

The broad-headed ceratophryine leptodactylids (especially *Ceratophrys*) are cannibalistic, and the width of their gape is probably of importance in capturing and eating other frogs (Cochran, 1961; Noble, 1931). Many other frogs, having normal head widths are frequently cannibalistic (e.g., *Rana catesbeiana*) but frog-eating habits are most often attributed to those frogs having large, broad-heads (*Pyxicephalus adspersa* of Africa is well-known in this regard). I examined the stomach contents of a few examples of broad-headed eleutherodactylines but found no frog remains. The frogs examined (and stomach contents) included one *E. cerastes* (large millipedes, spiders), one *E. nigerus* (small to large beetles, large spider), and three *E. sulcatus* (small to large beetles). The only notable point concerning the stomach contents is the relatively large size of the prey (relative to the size of the frogs). If we accept Hutchinson's (1959) argument of comparing trophic features (gape here), greater head width seems to be a means of affecting niche separation without becoming a much larger frog. However, quantitative data on prey size and the frequency of frog-eating by most anuran species in nature remains to be investigated.

The broad-headed eleutherodactylines are distributed largely allopatrically to the ceratophryine leptodactylids. Three species of *Ceratophrys* occur in northwestern South America. *Ceratophrys stolzmanni* occurs in arid to semi-arid habitats in northwestern Peru

and southwestern Ecuador (Peters, 1967), just south of the distribution areas of the Chocoan elements of the broad-headed eleutherodactylines (*E. biporcatus*, *E. bufoniformis*, *E. cerastes*, and *E. nigerus*). *Ceratophrys cornuta* is widely distributed in the Amazon drainage, ranging westward to the base of the Andes in at least Ecuador, where it occurs syntopically with *E. sulcatus*. Its distributional area extends much farther to the east than does that of *E. sulcatus*, and it presently appears that *E. sulcatus* is much more abundant in Ecuador than is *C. cornuta*, which is best described as rare in Ecuador. To the south and east, *C. cornuta* is evidently more abundant, as judged from the length of series collected in those areas contrasted to the widely disperse (spatial and temporal) collections of the species in Ecuador. *Ceratophrys calcarata* occurs in the Santa Marta region of Colombia and has also been reported from the upper Orinoco (Rivero, 1961) in Venezuela. Both of these areas are allopatric to the distribution areas of the several broad-headed eleutherodactylines.

Eleutherodactylus maussi of the Coastal Range of Venezuela is widely separated geographically from the remaining species of broad-headed eleutherodactylines. *Eleutherodactylus cornutus* and *E. sulcatus* are parapatrically distributed in eastern Ecuador (*cornutus* at higher elevations) and *E. sulcatus* ranges south into central Peru and east to western Brasil. *Amblyphryne ingeri* occurs at elevations of 2000 m in Andean Colombia but is not sympatric with any other broad-headed eleutherodactyline. The Pacific versant and lowlands of Colombia and northern Ecuador contain the richest fauna of broad-headed taxa. Data are rather sketchy at present but *E. cerastes* appears to occur at slightly higher elevations along the versant than do the other four species in the region, but co-occurs with *E. biporcatus* in Colombia and *E. nigerus* and *A. helonotus* in Ecuador. Two species (*E. biporcatus* and *E. bufoniformis*) are more clearly low elevation species than are the three intermediate elevation taxa (*A. helonotus*, *E. cerastes*, *E. nigerus*), but the several species may prove to be sympatric when more collecting has been done on the western Andean slopes. Although they may prove to be more generally sympatric, they are probably ecologically segregated in that *E. bufoniformis*, *E. nigerus*, and *A. helonotus* have lateral fringes on the toes and are likely to occur in greater proximity to streams than *E. biporcatus* and *E. cerastes* (species lacking toe fringes). The two species of *Eleutherodactylus* with toe fringes are dichopatrically distributed (*E. bufoniformis* in Panama and northern Chocoan Colombia; *E. nigerus* in northern Chocoan Ecuador) as are the two species lacking toe fringes (*E. biporcatus* ranging from Honduras to northern Chocoan Colombia; *E. cerastes* from central Chocoan Colombia to Ecuador). The allopatric distributions of these species pairs is suggestive of recent separation, ecologic

complimentarity, and may reflect the Pleistocene contractions of forested habitats into forest islands (Haffer, 1969), now represented as "wet" islands in the lowland, humid forests.

Several authors have commented on the generic status of the broad-headed eleutherodactylines (e.g. Myers, 1962; Rivero, 1961). The nominate genera having as type-species one of the members of this complex include, in addition to *Amblyphrymnus*, *Ctenocranius* Melin (type-species by subsequent designation, Myers, 1962, *Limnophys cornutus* Jiménez de la Espada), *Limnophys* Jiménez de la Espada (type-species by subsequent designation, Myers, 1962, *L. cornutus* Jiménez de la Espada), and *Strabonantis* Peters (type-species by monotypy, *S. biporcatus* Peters). All of the generic names excepting *Amblyphrymnus* are based on taxa in the *biporcatus* group. No generic name is available for the *sulcatus* group although Melin may have intended *Ctenocranius* for a *sulcatus*-type frog rather than the *biporcatus*-frog designated the type-species by Myers (1962).

The broad-headed eleutherodactylines with cranial crests have constituted a putative species-group or genus since 1864. The condition of head width is diagnostic but the presence of cranial crests, while characteristic, is not. These frogs tend to have narrow digit tips (i.e., lack pads), especially on the hands, have prominent tympana, and reach comparatively large size. Except for head width, these traits characterize but do not diagnose the putative group. To recognize a single and separate genus for the broad-headed eleutherodactylines requires that the genus be founded on the basis of a single trait—head width—and ignores the variation in characteristics within the group. Furthermore, the broad-headed condition is approached by two species of "normal" head width *Eleutherodactylus*—*E. anomalus* and *E. laticeps*. Cladistically (Fig. 17), the *E. sulcatus* group and *Amblyphrymnus* could be united as a generic group contrasting with the more heterogeneous *E. biporcatus* group, but the distinctions between the two units (OTUs 1-4 and OTUs 5-9) are few. In keeping with my generally conservative approach to genera (Lynch, 1971) and the use of derived character-states (loss of digital discs in *Amblyphrymnus*), I continue to include the *biporcatus* and *sulcatus* groups in *Eleutherodactylus*.

SPECIMENS EXAMINED (From South America)

Amblyphrymnus helonotus (2). ECUADOR, Prov. Pichincha: Mindo, USNM 195784; Rio Pitzara, BMNH 1970.178.

Amblyphrymnus ingeri (10). COLOMBIA, Depto. Antioquia: El Clara Creek, AMNH 39978-80; Medellin, AMNH 38639, 38649. Depto. Cundinamarca: Bogotá, BMNH 69.7.25.11; 8 km S Gachalá, San Isidro, FMNH 81915. Depto. Magdalena: west side of Sierra Nevada, Santa Marta, MCZ 17577. Depto. Tolima: Guindio mountains, MCZ 8237-38.

Eleutherodactylus biporcatus (21). COLOMBIA. Depto. Caldas: Pueblo

Rico, Santa Cecilia, 800 m, FMNH 54591. *Dept. Choco*: Alto del Buey, north slope, 300-1070 m, LACM 73154-57, 73177-80; Camino de Yupe, 350-625 m, LACM 73153, 73167-76. *Dept. Valle*: Raposa River Station, Rio Raposa, USNM 151447, UMMZ 132814.

Eleutherodactylus bufoniformis (6). COLOMBIA, *Dept. Choco*: Camino de Yupe, 350-500 m, LACM 73245-46; upper Rio del Valle, 50 m, LACM 73247; Alto del Buey, north slope, 300-420 m, LACM 73248-49; *Dept. Valle*: Buenaventura, BMNH 95.11.16.54/1947.2.15.68 (holotype).

Eleutherodactylus cerastes (20). COLOMBIA, *Dept. Cauca*: Pueblo Rico, 1580 m, BM 1910.7.11.61-62; El Tambo, La Costa, 1000 m, KU 144992-93; El Tambo, Munchique, 1000 m, KU 144994. *Dept. Valle*: 13 km W Dagua, Rio Anchicayá drainage, 850-1200 m, AMNH 88062.

ECUADOR. *Imbabura Prov.*: Lita, Rio Mira USNM 195786-88, 195795. *Pichincha Prov.*: Pachijal, USNM 195789-93; Palma Real, 195794; Rio Pitzara, USNM 195796(3); road from Pacto to Rio Guayllabamba, USNM 195797.

Eleutherodactylus cornutus (43). ECUADOR. USNM 167431. *Prov. Morona-Santiago*: Cutucu mountains, east of Macas, 1800-2000 m, AMNH 39499; Macuma, USNM 167401-08; Miazal, 167409-27. *Prov. Napo*: S slope Cordillera del Dué above Rio Coca, 1150 m, KU 123447-48; Loreto, USNM 167428; Rio Azuela, 1740 m, KU 143350; Cerro Sumaco, AMNH 22265-70; S slope Cerro Sumaco, USNM 167429. *Prov. Pastaza*: Canelos, USNM 167430. *Prov. Tungurahua*: El Topo, 1270 m, BM 1912.11.1.57; Mirador, Baños, 1500 m, BM 94.10.30.44.

Eleutherodactylus maussi (46). VENEZUELA, *Estado Aragua*: Rancho Grande, AMNH 70533-52, 70554-58, MCZ 50701-02, UMMZ 113932(5), 113933-34, 113935(2), 113936-41, 122376-77. *Estado Carabobo*: Puerto Cabello, MCZ 10178 (cotype); San Esteban, UMMZ 56474.

Eleutherodactylus necerus (4). ECUADOR, *Prov. Pichincha*: Mindo, USNM 195798; road from Pacto to Rio Guayllabamba, USNM 195851; Rio Blanco, near mouth Rio Yambi, USNM 195852; Rio Lelia, tributary of Rio Toachi, USNM 195799.

Eleutherodactylus sulcatus (93). BRASIL, *Estado Amazonas*: Taracuá GNM 494 (holotype *Ctenocranius koki*). ECUADOR, *Prov. Morona-Santiago*: Miazal, USNM 167452-60; Valle Santiago, MZS 2930(2) (cotypes, larger here designated lectotype, *Hylodes macrocephalus*). *Prov. Napo*: Limón Cocha, 300 m, LACM 72161-62, UIMNH 55796; Loreto, USNM 167433-44; Payamino, USNM 167451; Puerto Libre, 570 m, KU 123585-87; Rio Cotopino, USNM 167432; upper Rio Napo, 500 m, UMMZ 92111(2), 92114; Rio Suno, UMMZ 92112; San José, Abayo Oriente, AMNH 22176, 22181, 22184; Santa Cecilia, 340 m, AUM 7850-54, KU 108989, 123574-84; S slope Cerro Sumaco, USNM 167445-50. *Prov. Pastaza*: Canelos to Marañon, Rio Bobonaza, MCZ 19640-41, USNM 139897; Don Tomás, 5 km S Montalvo, USNM 167462; Pacayacu, USNM 167466-68; region of Puyo, USNM 167469-70; 9 km SE Puyo, UMMZ 126820; Rio Arajuno headwaters, USNM 167464; Rio Capahuari headwaters, USNM 167463; Rio Pindo, near town of Rio Tigre, USNM 167461; mouth of Rio Shiona at Rio Conambo, USNM 167465. PERU, *Dept. Amazonas*: Rio Cenipa, Ayendama, AMNH 42272; mouth of Rio Santiago, AMNH 42304. *Dept. Junín*: Chanchamayo, AMNH 42894. *Dept. Loreto*: Centre Union, TCWC 41699, 41738; Iquitos, AMNH 42293; Moropon, TCWC 39215-16; Manseriche range, head of Rio Caterpisa, 1500 ft., AMNH 42046; Nauta, ANSP 11385 (holotype, *Hylodes sulcatus*); upper Rio Cushabatay, AMNH 42922; Rio Sapo, Rio Portongo, AMNH 43391; Rio Tampo (Tambo), AMNH 42091-92; upper Rio Utoquinea, AMNH 43136, 43377. *Dept. San Martín*: Rio Huallaga, Achinamisa, AMNH 42503.

SUMMARY

The broad-headed eleutherodactyline frogs (head width 45-65% snout-vent length) occur in forested habitats from Honduras to Venezuela and Peru. Nine species in two genera are recognized. Seven species are placed in two species groups of *Eleutherodactylus*. The *biporcatus* group includes five species: *biporcatus*, *bufoniformis*, *cerastes* sp. nov., *cornutus*, and *necerus* sp. nov. The *sulcatus* group includes two species: *maussi* and *sulcatus*. Two species of *Amblyphrymnus* are recognized: *helonotus* sp. nov. and *ingeri*.

Based on an analysis of the characteristics evident among the nine species, the relationships of the taxa are examined cladistically. The cladistic analysis suggests that this complex of frogs is derived from frogs of the *fitzingeri* group. The discless frogs of the genus *Amblyphrymnus* are advanced representatives of the broad-headed group and differ from *Eleutherodactylus* in having lost digital discs. If the broad-headed frogs with digital discs are accorded generic recognition, the generic name would be *Strabomantis*.

Most published records of *E. cornutus* apply to *Amblyphrymnus ingeri* (Colombian records) or *E. sulcatus* (Ecuador, Peru). *Limnophys napaeus* Jiménez de la Espada is removed from the synonymy of *E. biporcatus* and placed in the synonymy of *E. cornutus*. *Hyloides macrocephalus* Peracca and *Ctenocranius koki* Melin are assigned to the synonymy of *E. sulcatus*.

Three new species are named. *Amblyphrymnus helonotus* from the Pacific Andean versant of Ecuador differs from *A. ingeri* in lacking osteoderms, lacking a squamosal-maxillary connection, having arch-like prevomerine odontophores instead of triangular processes, lower cranial crests, no tarsal fold, and in coloration and proportions. *Eleutherodactylus cerastes* from the Pacific Andean versant of Colombia and Ecuador differs from *E. biporcatus* in having an elongate eyelid tubercle, arch-like prevomerine processes, and smaller tympana; *cerastes* differs from *cornutus* in lacking tarsal folds and lateral fringes on the toes and in having pale spots of the concealed thigh surfaces. *Eleutherodactylus necerus* from the Pacific Andean versant of Ecuador differs from *E. bufoniformis* in lacking toe webbing, having arch-like prevomerine processes, and in lacking brown mottling on the venter.

Broad-headed eleutherodactyline species are primarily parapatrically distributed among themselves as well as relative to other broad-headed leptodactylids, especially *Ceratophrys*. *Eleutherodactylus biporcatus* and *E. bufoniformis* are sympatric over much of Chocoan Colombia and forested Panama. *Amblyphrymnus helonotus*, *Eleutherodactylus cerastes*, and *E. necerus* may prove to be sympatric on the Andean slopes of western Ecuador. Between subfamilies (Ceratophryinae and Telmatobiinae), sympatric occurrence of *Ceratophrys cornuta* and *Eleutherodactylus sulcatus* constitutes

the only contradiction of this generalization. The largely parapatric pattern of distribution is suggestive of potential competition among broad-headed leptodactylids.

RESUMEN

Las ranas eleutherodactylinas con cabezas ancha (ancha de la cabeza equal 45-65 porcent hocico-ano longitud) viven en bosques entra Honduras hasta Venezuela y el Peru. Nueve especies de dos géneros son reconocadas. Siete especies son colocadas en dos especies-grupos del género *Eleutherodactylus*. El grupo *biporcatus* contiene cinco especies: *biporcatus*, *bufoniformis*, *cerastes* esp. nov., *cornutus*, y *necerus* esp. nov. El grupo *sulcatus* contiene dos especies: *maussi* y *sulcatus*. Dos especies del género *Amblyphryalus* son reconocadas—*helonotus* esp. nov. y *ingeri*.

Las afinidades de los nueve especies son examinadas cladísticamente. Es análisis se indica que esta colección de ranas se derivadas de ranas del grupo *fitzingeri* (género *Eleutherodactylus*). Las ranas que faltan discos (género *Amblyphryalus*) son avanzado especies de los grupos con ancha cabezas y son distinto de *Eleutherodactylus* porque ellos faltan todos discos de los dedos. Si las ranas con cabezas ancha y discos de los dedos se acomodado reconocimiento genérico, el nombre genérico estará *Strabomantis* (en lugar de dos especies-grupos de *Eleutherodactylus*).

La parte mayor de las anotaciones publicadas de *E. cornutus* son actualamente *Amplyphryalus ingeri* (anotaciones colombianos) o *E. sulcatus* (anotaciones ecuatorianos y peruanos). *Limnophys naeaeus* no es un sinónimo de *E. biporcatus* pero es un sinónimo de *E. cornutus*. *Hyloides macrocephalus* y *Ctenocranius koki* son colocadas en la sinónimia de *E. sulcatus*.

Tres especies nuevas se llaman. *Amblyphryalus helonotus* de las faldas andinas pacifico del Ecuador se distinguido de *A. ingeri* en faltando osteodermos, faltando un articulación escamoso-maxilar, en teniendo odontoforos prevomerinos arco-semejante en lugar de protuberancias triangular, crestas del cráneo más bajo, no plieque tarsal, y en coloración y proporciones. *Eleutherodactylus cerastes* de las faldas andinas pacifico de Colombia y Ecuador se distinguido de *E. biporcatus* en teniendo un tuberculo párpado bien alargado, protuberancias prevomerinos arco-semejante, y un tímpano menor; *cerastes* se distinguido de *cornutus* en faltando plieques tarsal y orillas laterales en los dedos (pes), y en teniendo puntos pálidos en los superficies del muslo callado. *Eleutherodactylus necerus* de las faldas andinas pacifico de Ecuador se distinguido de *E. bufoniformis* en faltando membranas interdigital de pes, en teniendo odontoforos prevomerinos arco-semejante en lugar de protuberancias triangular, y en teniendo un abdomen blanco (en lugar de moteado con moreno).

En general, los especies eleutherodactylinos con cabezas ancha tienen distribuciones parapátricos entre ellos mismos y tambien relativo a otra leptodactylinos con cabezas ancha, especialmente *Ceratophrys*. *Eleutherodactylus biporcatus* y *E. bufoniformis* son macrosimpátrico en Colombia occidental y Panamá. *Amblyphryalus helonotus*, *Eleutherodactylus cerastes*, y *E. necerus* son encontrado tal vez simpátricamente en las faldas andinas pacifico en Ecuador. Entre los subfamilias (Ceratophryinae y Telmatobiinae), suceso simpátrico de *Ceratophrys cornuta* y *Eleutherodactylus sulcatus* constituye el contradicción solo de este generalización. El modelo de distribución (principalmente parapátrico) es sugestivo de competición potencial entre los leptodactylinos con cabezas anchas.

LITERATURE CITED

ANDERSSON, L. G. 1945. Batrachians from east Ecuador collected 1937, 1938 by Wm. Clarke-Macintyre and Rolf Blomberg. *Arkiv för Zoologi*, 37A (2):1-88.

BOETTGER, O. 1893. Reptilien und Batrachier aus Venezuela. *Ber. Senckenb. Naturf. Ges.*, 1893:35-42.

BOULENGER, G. A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collections of the British Museum. 2nd ed. 503 pp.

BOULENGER, G. A. 1896. Descriptions of new reptiles and batrachians. *Ann. Mag. Nat. Hist.*, (6)17:16-21.

BROCCHI, P. 1882. Etude des batraciens de l'Amérique Centrale. In, *Mission scientifique au Mexique et dans l'Amérique Centrale; Recherches zoologiques*, pt. 3, sec. 2, 122 pp.

CAMIN, J. H., SOKAL, R. R. 1965. A method for deducing branching sequences in phylogeny. *Evolution*, 19:311-26.

COCHRAN, D. M. 1961. Living amphibians of the world. Doubleday & Company, Inc. 199 pp.

COCHRAN, D. M., GOIN, C. J. 1961. A new genus and species of frog (Leptodactylidae) from Colombia. *Fieldiana, Zool.*, 39:543-46.

COCHRAN, D. M., GOIN, C. J. 1970. Frogs of Colombia. *Bull. U.S. Natl. Mus.* (288). 655 pp.

COPE, E. D. 1866. On the structures and distribution of the genera of the ariciferous Anura. *Journ. Acad. Nat. Sci. Philadelphia*, 6:67-112.

COPE, E. D. 1874. On some Batrachia and Nematognathi brought from the Upper Amazon by Professor Orton. *Proc. Acad. Nat. Sci. Philadelphia*, 26:120-32.

COPE, E. D. 1875. On the Batrachia and Reptilia of Costa Rica. *Journ. Acad. Nat. Sci. Philadelphia*, (2) 8:93-157.

COPE, E. D. 1877. Tenth contribution to the herpetology of tropical America. *Proc. Amer. Philos. Soc.*, 17:85-98.

COPE, E. D. 1893. Second addition to a knowledge of the batrachians and Reptilia of Costa Rica. *Ibid.*, 31:333-47.

DUNN, E. R. 1931. The amphibians of Barro Colorado Island. *Occ. Papers Boston Soc. Nat. Hist.*, 5:403-21.

DUNN, E. R. 1944. Herpetology of the Bogotá area. *Rev. Acad. Colombiana Cien. Ex. Fís. Nat.*, 6:68-81.

GINES, H. 1959. Familias y géneros de Anfibios—Amphibia—de Venezuela. *Mem. Soc. Cienc. Nat. LaSalle*, 19:85-146.

GORHAM, S. W. 1966. Liste der rezenten Amphibien und Reptilien. Ascaphidae. Leiopelmatidae. Pipidae, Discoglossidae, Pelobatidae, Leptodactylidae, Rhinophrynidae. *Des Tierreich*, 85:222 pp.

GUNTHER, A. C. L. G. 1901. *Reptilia and Batrachia*, 326 pp., *In*, Godman and Salvin, eds., *Biologia Centrali-Americanana*. London.

HAEFFER, J. 1969. Speciation in Amazonian forest birds. *Science*, 165:131-37.

HEATWOLE, H. 1962. Contributions to the natural history of *Eleutherodactylus cornutus maussi*. *Stahlia*, *Misc. Papers*, 2:1-11.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals. *Amer. Natur.*, 93:145-59.

INGER, R. F. 1958. Comments on the definition of genera. *Evolution*, 12: 370-84.

JIMÉNEZ DE LA ESPADA, D. M. 1870. *Faunae neotropicalis species quaedam nondum cognitae. Amphibia*. *Jorn. Sci. Math. Lisbon*, 3:58-65.

JIMÉNEZ DE LA ESPADA, D. M. 1872. Nuevos batracios Americanos. *Anales Soc. Español. Hist. Nat.*, 1:85-88.

JIMÉNEZ DE LA ESPADA, D. M. 1875. Vertebrados del viaje al Pacífico verificado de 1862 á 1865 por una comisión de naturalistas enviada por el gobierno español. Batracios. Madrid. 207 pp., 6 pls.

LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Univ. Kansas Publs. Mus. Nat. Hist., Misc. Publs.*, (53):1-238.

LYNCH, J. D. 1973. A new narrow-toed frog from Andean Ecuador (Leptodactylidae: *Eleutherodactylus*). *Copeia*, 1973(2):222-25.

MELIN, D. 1941. Contributions to the knowledge of the Amphibia of South America. *Medd. Göteborgs Mus. Zool. Avdel.*, 88:1-71.

MYERS, G. S. 1962. The American leptodactylid frog genera *Eleutherodactylus*, *Hylodes* (= *Elosia*), and *Caudiverbera* (= *Calytocephalus*). *Copeia*, 1962(1):195-202.

NIEDEN, F. 1923. Anura I. Subordo Aglossa und Phaneroglossa. *Sectio I Arcifera. Das Tierreich*, 46:584 pp.

NOBLE, G. K. 1918. The amphibians collected by the American Museum expedition to Nicaragua in 1916. *Bull. Amer. Mus. Natur. Hist.*, 38:311-47.

NOBLE, G. K. 1931. The biology of the Amphibia. McGraw-Hill, New York. 577 pp.

PERACCA, M. G. CONTE DE. 1904. Viaggia del Dr. Enrico Festa nell'Ecuador e regioni vicine. Rettili ed. Anfibi. *Boll. Mus. Zool. Torino*, 19(465):1-41.

PERACCA, M. G. CONTE DE. 1904. Reptiles et Batrachians de Colombie. *Mem. Soc. Neuchâtel Nat. Hist.*, 5:96-111.

PETERS, J. A. 1955. Herpetological type localities in Ecuador. *Rev. Ecuat. Ent.-Par.*, 2(3-4):335-52.

PETERS, J. A. 1967. The generic allocation of the frog *Ceratophrys stolzmanni* Steindachner, with the description of a new subspecies from Ecuador. *Proc. Biol. Soc. Washington*, 80:105-12.

PETERS, W. 1864. Über eine neue Schlangengattung, *Styphorhynchus*, und verschiedene andere Amphibien des zoologischen Museums. *Monatsb. d.k. Preuss. Akad. Wiss. Berlin*, 1863:399-413.

PETERS, W. 1874. Über eine neue Schildkrotenart, *Cinosternon Effeldtii* und einige andere neue oder weniger bekannte Amphibien. *Ibid.*, 1873: 603-18.

RIVERO, J. A. 1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool.*, 126:1-207.

TAYLOR, E. H. 1952. The frogs and toads of Costa Rica. *Univ. Kansas Sci. Bull.*, 35:577-942.

TAYLOR, E. H. 1955. Additions to the known herpetological fauna of Costa Rica with comments on other species. No. II. *Ibid.*, 37:499-575.